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First U.S. Commissioner
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of *Fishery Bulletin*

Abundance estimates of cetaceans from a line-transect survey within the U.S. Hawaiian Islands Exclusive Economic Zone

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Abstract—A ship-based line-transect survey was conducted during the summer and fall of 2010 to obtain abundance estimates of cetaceans in the U.S. Hawaiian Islands Exclusive Economic Zone (EEZ). Given the low sighting rates for cetaceans in the study area, sightings from 2010 were pooled with sightings made during previous line-transect surveys within the central Pacific for calculating detection functions, which were estimated by using a multiple-covariate approach. The trackline detection probabilities used in this study are the first to reflect the effect of sighting conditions in the central Pacific and are markedly lower than estimates used in previous studies. During the survey, 23 cetacean species (17 odontocetes and 6 mysticetes) were seen, and abundance was estimated for 19 of them (15 odontocetes and 4 mysticetes). Group size and Beaufort sea state were the most important factors affecting the detectability of cetacean groups. Across all species, abundance estimates and coefficients of variation range from 133 to 72,528 and from 0.29 to 1.13, respectively. Estimated abundance is highest for delphinid species and lowest for the killer whale (*Orcinus orca*) and rorqual species. Overall, cetacean density in the Hawaiian Islands EEZ is low in comparison with highly productive oceanic regions.

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Twenty-five cetacean species are known to occur in the U.S. Hawaiian Islands Exclusive Economic Zone (EEZ). Before the 2000s, most research on cetaceans in Hawaii focused on humpback whales (*Megaptera novaeangliae*) (e.g., Herman and Antinoja, 1977; Mobley et al., 1999) and spinner dolphins (*Stenella longirostris*) (e.g., Norris and Dohl, 1980; Norris et al., 1994) because individuals of these species are concentrated (seasonally in the case of humpback whales) in nearshore waters of the main Hawaiian Islands. Although there were studies of rarer or less accessible species, such as the pygmy killer whale (*Feresa attenuata*) and short-finned pilot whale (*Globicephala macrorhynchus*) (e.g., Pryor et al., 1965; Shane and McSweeney, 1990), more frequent and directed surveys for a variety of species were not initiated until 2000 (e.g., Baird, 2005; McSweeney et al., 2007; Baird et al., 2009). Although that recent research has provided significant insight into the occurrence, distribution, abundance, stock structure, and social organization of cetaceans in Hawaii waters, the surveys were focused primarily on nearshore odontocete species associated with the main Hawaiian Islands.

In 2002, the Southwest Fisheries Science Center (SWFSC) of the National Marine Fisheries Service (NMFS) conducted the first Hawaiian Islands Cetacean and Ecosystem Assessment Survey (HICEAS), a ship-based line-transect survey designed to estimate the abundance of cetaceans in the entirety of the Hawaiian Islands EEZ. During the HICEAS in 2002, 23 cetacean species (18 odontocetes and 5 mysticetes) were encountered, and the abundance of 19 species (18 odontocetes and 1 mysticete) was estimated (Barlow, 2006). These estimates represented the first abundance estimates for most cetacean stocks in Hawaii waters and were incorporated in the stock assessment

reports produced by NMFS in accordance with the Marine Mammal Protection Act of 1972 (e.g., Carretta et al., 2005).

Abundance estimates used in marine mammal stock assessment reports are considered outdated after 8 years (NMFS[1]). Therefore, a second HICEAS was carried out in 2010, as a collaborative effort between the SWFSC and the NMFS Pacific Islands Fisheries Science Center (PIFSC), with objectives, timing, and methods comparable to those of the HICEAS conducted in 2002. However, adjustments were made to the data collection protocol for the false killer whale (*Pseudorca crassidens*) during the HICEAS in 2010—changes that necessitated a separate and specialized abundance analysis for this species (Bradford et al., 2014, 2015). The objective of the present study was to estimate the abundance of the remaining cetacean stocks encountered during the HICEAS in 2010. Although the resulting abundance estimates are specific to cetacean stock assessment in the Hawaiian Islands EEZ, the analytical methods used are applicable to line-transect surveys of cetaceans in other regions.

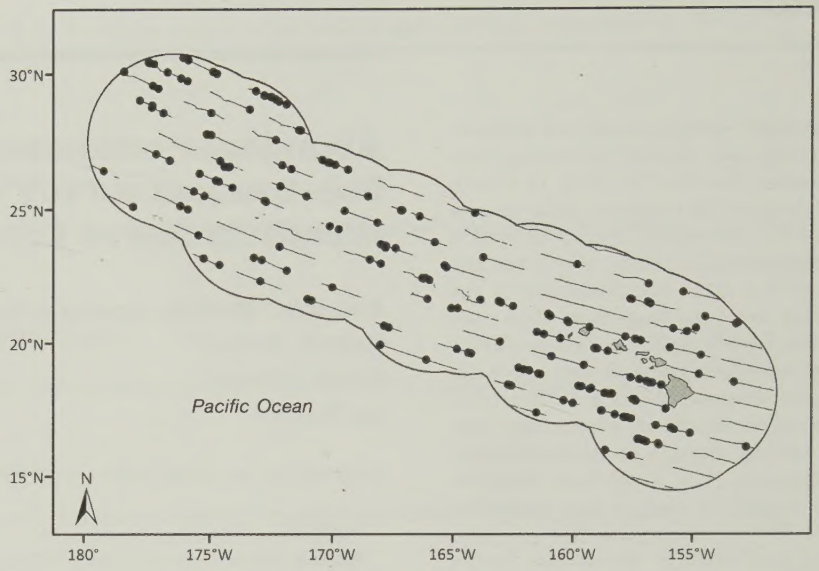

Figure 1

Locations of cetacean groups (black dots; n=198) sighted by observers on systematic line-transect survey effort (fine lines) in Beaufort sea states 0–6 within the U.S. Hawaiian Islands Exclusive Economic Zone (thick black outline) during the Hawaiian Islands Cetacean and Ecosystem Assessment Survey in 2010. Nine sightings were of mixed-species groups, in which at least 2 species were seen. The main Hawaiian Islands are shown in gray with a thin black outline.

Materials and methods

Data collection

The HICEAS in 2010 was conducted aboard two 68-m NOAA research vessels within the Hawaiian Islands EEZ during the summer and fall (Fig. 1) The study area was surveyed from the NOAA ship *McArthur II* from 13 August to 1 December 2010 and from the NOAA ship *Oscar Elton Sette* from 2 September to 29 October 2010. The survey design of the HICEAS in 2010 was similar to that of the HICEAS in 2002 (Barlow, 2006). That is, both surveys were based on a grid of parallel transect lines that provided comprehensive coverage of the study area. These transect lines were the basis for the daily tracklines of each ship and were oriented from west-northwest to east-southeast in order to minimize the effects of dominant regional swells generated by northeasterly to easterly trade winds. The grid used for the HICEAS in 2002 was established by positioning transect lines parallel to a randomly placed baseline at spacing intervals of 85 km. Transect lines for the HICEAS in 2010 were placed midway between each of the lines used in 2002 to maximize spatial coverage of the Hawaiian Islands EEZ over the 2 surveys. The survey effort in 2002 was stratified, and a higher density of transect lines occurred within 140 km of the main Hawaiian Islands. This stratification was not maintained for the HICEAS in 2010. Therefore, the systematic survey effort in 2010 was roughly uniform throughout the study area. The survey speed of both ships was 18.5 km/h (10 kt).

Although transits to and from ports and circumnavigations of the Northwestern Hawaiian Islands were not a part of the systematic survey grid, the observers remained on-effort and followed standard observation protocols during these periods. This nonsystematic effort differed from effort during periods when the observers were not following standard observation protocols—periods that were considered to be off-effort (e.g., during inclement weather or diversions from the tracklines). Sightings of cetaceans made during nonsystematic effort and off-effort were not applied to the density estimator (see Eq. 1 later in this section) because those sightings were not detected on the systematic transect lines. However, sightings made during nonsystematic effort were used in the estimation of species detection functions because the observation protocols did not differ between systematic and nonsystematic efforts.

[1] NMFS (National Marine Fisheries Service). 2005. Revisions to guidelines for assessing marine mammal stocks, 24 p. [Available at website.]

The observation methods used during the HICEAS in 2010 were developed by the SWFSC and have been in use for the last 3 decades (e.g., Barlow, 2006). To summarize these methods, observation teams consisted of 6 observers who rotated through 3 roles (port and starboard observers and a data recorder) and searched for cetaceans 180° forward of the vessel by using 25× binoculars (port and starboard observers) and with unaided eyes (data recorder) from the flying bridge (approximately 15 m above the sea surface on both ships). When cetaceans were sighted within 5.6 km (3 nmi) of the trackline by 1 of the 3 on-effort observers, systematic search effort was suspended and the ship diverted from the trackline toward the sighting so that species, species composition (for mixed-species groups), and group size could be determined. In addition to basic environmental data (e.g., Beaufort sea state, swell height, and visibility), data collected for each sighting included the time, location, initial bearing and radial distance to the cetacean group (used to calculate the perpendicular distance of the sighting to the trackline), species identity, proportion of each species present (mixed-species groups), and identity of observers and their independent estimates of sighting group size (recorded as a "best," "high," and "low" estimate for each observer). If species identity could not be determined for a sighting, the lowest possible taxonomic category was applied (see Table 1 for the categories relevant to the HICEAS in 2010). After the identification of species and estimation of group size for some sightings, depending on weather, animal behavior, and research priorities, a small boat was launched to collect photo-identification images and biopsy samples.

Additionally, an acoustics team worked independently from the observers, detecting cetacean vocalizations by using a hydrophone array towed behind each ship during daylight hours. This team did not inform the observer team of acoustic detections. The abundance estimation reported in the present study is based solely on the sightings made by the observers. That is, cetaceans that were detected only acoustically were not included in the abundance analysis. The acoustic detections from the HICEAS in 2010 are currently being processed for future line-transect analyses.

Estimation of abundance

Cetacean abundance in the Hawaiian Islands EEZ was estimated by using a multiple-covariate line-transect approach (Buckland et al., 2001; Marques and Buckland, 2004). Specifically, detection functions were modeled as a function of factors known to affect the detectability of cetacean groups. Sighting rates are low in the Hawaiian Islands EEZ (Barlow, 2006), and as were the sample sizes during the HICEAS in 2002, sample sizes for each species sighted during the HICEAS in 2010 were inadequate for modeling the detection functions. Therefore, as with analysis of sightings from the HICEAS in 2002 (Barlow, 2006), sightings from the HICEAS in 2010 were pooled with sightings collected during previous NMFS ship-based line-transect surveys of the eastern Pacific. The estimation of detection functions for the HICEAS in 2002 incorporated sightings made throughout the eastern Pacific during SWFSC surveys conducted from 1986 through 2002, but the sighting pool for the analysis of the 2010 data was restricted to sightings made in the central Pacific (defined here as the area of the eastern Pacific north of 5°S, south of 40°N, west of 120°W, and east of 175°E) during SWFSC and PIFSC surveys from 1986 through 2010. The pooled sightings (collected during both systematic and nonsystematic efforts) were limited to the central Pacific to minimize heterogeneity resulting from geographical differences in species associations and behavior—complex factors that can be difficult to represent as covariates.

Despite survey data from the present study being pooled with previous survey data, sample sizes for most species remained insufficient for estimating the detection function. Therefore, sightings of species with similar detection characteristics (e.g., size, surface behavior, group sizes) were also combined for modeling the detection function. Specifically, 6 species pools were formed: 1) small delphinids with relatively large group sizes; 2) small and medium delphinids with relatively small group sizes; 3) large delphinids and co-occurring beaked whales with similar behavior (Barlow, 2006); 4) large and highly conspicuous odontocetes (Barlow et al., 2011a); 5) beaked whales with relatively small group sizes; and 6) baleen whales (see Table 2 for the composition of each species pool).

A half-normal model was used to evaluate the detection probabilities for the sightings in each species pool as a function of perpendicular distance from the trackline and of relevant covariates. Only half-normal models were used because of the greater stability they exhibit when fitting sighting data for cetaceans (Gerrodette and Forcada, 2005). The 5–10% most distant sightings in each species pool were truncated to improve model fit (Buckland et al., 2001), although no truncation distance exceeded the 5.6-km limit at which the ship would not divert from the trackline for a sighting. Covariate models were built by using a forward stepwise procedure and were selected by using Akaike's information criterion corrected for a small sample size (AICc; Hurvich and Tsai, 1989).

Although several factors have the potential to affect the perpendicular sighting distances to cetaceans (Barlow et al., 2001), a smaller set of covariates identified as important and robust in estimating detection probabilities (Barlow et al., 2011a) was considered for analysis in the present study. Of the covariates identified by Barlow et al. (2011a), *visibility* and *swell anomaly* could not be tested because these variables were not recorded during SWFSC surveys before 1991, and *region* was not applicable because the pooled sightings were restricted to the central Pacific. The remaining covariates evaluated were *Beaufort* (Beaufort sea state, treated as a continuous variable), *group size* (the natural logarithm of the sighting group size, which in-

Table 1

Names and number of sightings of cetacean species observed in the U.S. Hawaiian Islands Exclusive Economic Zone during the Hawaiian Islands Cetacean and Ecosystem Assessment Survey in 2010. Stock names refer to those used in the National Marine Fisheries Service stock assessment reports (Carretta et al., 2014). N_{TOT} is the number of systematic, nonsystematic, and off-effort sightings (n=398); N_{SYS} is the number of sightings made while on systematic effort in Beaufort sea states 0–6 (n=211); and N_{EST} is the number of sightings made while on systematic effort that were within the analytical truncation distance and, therefore, used in the abundance estimation (n=177). The abundance of some species could not be estimated (N/A). NWHI=Northwestern Hawaiian Islands.

Common name	Scientific name	Stock name	N_{TOT}	N_{SYS}	N_{EST}
Pantropical spotted dolphin	*Stenella attenuata*	Pelagic	12	11	10
Striped dolphin	*Stenella coeruleoalba*	Hawaii	25	20	18
Spinner dolphin	*Stenella longirostris*	Pelagic	4	0	N/A
Rough-toothed dolphin	*Steno bredanensis*	Hawaii	24	8	8
Bottlenose dolphin	*Tursiops truncatus*	Pelagic	19	7	6
Risso's dolphin	*Grampus griseus*	Hawaii	10	9	9
Fraser's dolphin	*Lagenodelphis hosei*	Hawaii	4	3	3
Melon-headed whale	*Peponocephala electra*	Hawaiian Islands	1	1	1
Pygmy killer whale	*Feresa attenuata*	Hawaii	5	4	4
False killer whale[1]	*Pseudorca crassidens*	Pelagic and NWHI	14	6	6
Short-finned pilot whale	*Globicephala macrorhynchus*	Hawaii	36	15	11
Killer whale	*Orcinus orca*	Hawaii	1	1	1
Sperm whale	*Physeter macrocephalus*	Hawaii	41	26	23
Dwarf sperm whale	*Kogia sima*	Hawaii	1	0	N/A
Unidentified *Kogia*	*Kogia sima/breviceps*	N/A	1	0	N/A
Blainville's beaked whale	*Mesoplodon densirostris*	Hawaii	2	1	1
Cuvier's beaked whale	*Ziphius cavirostris*	Hawaii	23	2	2
Longman's beaked whale	*Indopacetus pacificus*	Hawaii	3	3	3
Unidentified *Mesoplodon*	*Mesoplodon* spp.	N/A	10	6	6
Unidentified beaked whale	Ziphiid whale	N/A	27	4	3
Minke whale	*Balaenoptera acutorostrata*	Hawaii	1	0	N/A
Bryde's whale	*Balaenoptera edeni*	Hawaii	32	19	19
Sei whale	*Balaenoptera borealis*	Hawaii	2	2	2
Fin whale	*Balaenoptera physalus*	Hawaii	2	1	1
Blue whale	*Balaenoptera musculus*	Western North Pacific	1	1	1
Humpback whale	*Megaptera novaeangliae*	Central North Pacific	1	1	N/A
Sei or Bryde's whale	*Balaenoptera borealis/edeni*	N/A	12	9	8
Unidentified rorqual	Balaenopterid whale	N/A	11	9	6
Unidentified small dolphin	Small delphinid	N/A	17	10	6
Unidentified medium dolphin	Medium delphinid	N/A	6	3	1
Unidentified large dolphin	Large delphinid	N/A	3	2	2
Unidentified dolphin	Delphinid	N/A	19	9	6
Unidentified small whale	Small whale or large dolphin	N/A	1	1	1
Unidentified large whale	Large baleen or sperm whale	N/A	8	6	N/A
Unidentified whale	Small or large whale	N/A	3	2	2
Unidentified cetacean	Cetacean	N/A	16	9	7

[1]Abundance estimation of the pelagic and NWHI stocks of false killer whales is covered in Bradford et al. (2014, 2015) and was not considered further in this study.

cludes the total number of individuals in mixed-species groups, treated as a continuous variable), *cruise number* (the number assigned to each survey on a given ship in a given year, treated as a categorical variable), *ship* (the survey ship, treated as a categorical variable), *year* (the survey year, treated as a categorical variable), and *species* (the most abundant species within a group, treated as a categorical variable). The categorical covariates were tested only if there were at least 10 observations for each factor level.

To correct for the tendency of individual observers to over- or underestimate group size, correction factors were applied to the "best" estimates of sighting group size made by observers who were calibrated during previous SWFSC surveys by a comparison of observer group size estimates and counts of the same cetacean groups from aerial photographs (Gerrodette and Forcada, 2005). An indirect regression-based calibration method was used to calibrate noncalibrated observers in relation to the calibrated observers (Barlow, 1995;

Table 2

Detection functions modeled by using pooled sightings collected in the central North Pacific during line-transect surveys conducted from 1986 through 2010 by the NOAA Southwest and Pacific Islands Fisheries Science Centers. The estimated detection functions are listed along with the associated factor levels used to test the *species* covariate (see text for covariate descriptions). N_{TOT} is the number of available systematic and nonsystematic sightings in Beaufort sea states 0–6, and N_{DET} is the number of sightings that fell within the analytical truncation distance (TD; in kilometers). If a model with an additional covariate was within 2 Akaike's information criterion (corrected for a small sample size) units of the best-fit covariate model, the second covariate is shown in parentheses.

Detection function	N_{TOT}	N_{DET}	TD	Covariates tested	Best-fit model
Pantropical spotted dolphin	274	247	4.5	*Beaufort, group size, species*	*Group size(+Beaufort)*
Pantropical spotted dolphin	83	73			
Other[1]	191	174			
Species pool 1	282	255	4.5	*Beaufort, group size, ship*	*Ship(+group size)*
Striped dolphin	249	223			
Fraser's dolphin	23	22			
Melon-headed whale	7	7			
Other	3	3			
Species pool 2	231	216	5.0	*Beaufort, group size, species*	*Group size+species*
Rough-toothed dolphin	58	55			
Bottlenose dolphin	56	50			
Risso's dolphin	64	61			
Pygmy killer whale	14	14			
Other	39	36			
Species pool 3	152	138	4.5	*Beaufort, group size, ship*	Null(+*ship*)
Short-finned pilot whale	138	126			
Longman's beaked whale	5	5			
Other	9	7			
Species pool 4	144	128	5.5	*Beaufort, group size, species*	Null(+*species*)
Killer whale	34	34			
Sperm whale	109	94			
Other[2]	1	0			
Species pool 5	143	136	5.0	*Beaufort, group size*	*Beaufort+group size*
Blainville's beaked whale	7	7			
Cuvier's beaked whale	46	43			
Unidentified *Mesoplodon*	39	39			
Unidentified beaked whale	50	46			
Other	1	1			
Species pool 6	150	139	5.0	*Beaufort, group size*	Null(+*Beaufort*)
Bryde's whale	81	77			
Sei whale	11	9			
Fin whale	5	5			
Blue whale	4	4			
Sei or Bryde's whale	44	39			
Other	5	5			
Unidentified rorqual	61	47	5.5	*Beaufort, group size*	Null
Unidentified dolphin	316	281	5.5	*Beaufort, group size, ship*	*Beaufort+group size*
Unidentified cetacean	162	144	5.5	*Beaufort, group size*	*Beaufort(+group size)*

[1] A justification for testing for a *species* effect on this single-species detection function is provided in the text.
[2] The "other" sighting in this pool was within the TD but was removed for other reasons (see text for details).

Barlow and Forney, 2007). Sighting group size used in detection function modeling was a weighted geometric mean of the calibrated "best" estimates of group size made by each observer for each sighting (weighted by the inverse of the mean squared estimation error).

To obtain the number of individuals of each species in sightings of mixed-species groups (as needed for density estimation, see the next paragraph), the sighting group size was multiplied by the proportion of each species present (averaged over all observers). For some sightings of mixed-species groups, the most abundant species within a sighted group was not one of the pooled species—an outcome that complicated the use of the *species* covariate. The factor level for these sightings was labeled as "other" to account for the collective influence of nonpooled species on the detection

function (Table 2). For the species pool that includes killer whales (*Orcinus orca*) and sperm whales (*Physeter microcephalus*), the low number of "other" sightings (n=1) prevented testing the *species* covariate. Upon further examination, this sighting was found to contain a species co-occurrence not observed in the Hawaiian Islands EEZ and not represented in any of the other pooled sightings. Therefore, this sighting was removed from the pool used to estimate the detection function so that a *species* effect could be evaluated. Although the sample size was sufficient to model the detection function of pantropical spotted dolphins (*Stenella attenuata*) separately, the *species* covariate and the "other" factor level were used to explore the influence of a large number of sightings in which the pantropical spotted dolphin was not the most abundant species.

Given the estimated covariate detection function and the sightings within the established truncation distance from the systematic effort during the HICEAS in 2010, the density (D) of each species was estimated by using a Horvitz–Thompson-like estimator (Marques and Buckland, 2004):

$$D = \frac{1}{2 \cdot L \cdot g(0)} \sum_{j=1}^{N} f(0,\boldsymbol{c}_j) \cdot s_j, \quad (1)$$

where L = the length of systematic-effort transect lines in the study area;
$g(0)$ = the probability of detection on the trackline;
$f(0,\boldsymbol{c}_j)$ = the probability density of the detection function evaluated at zero distance for sighting j with associated covariates $\boldsymbol{c}$;
s_j = the number of individuals of the species in sighting j; and
N = the number of sightings of the species during systematic-effort within the analytical truncation distance.

The value of $f(0,\boldsymbol{c}_j)$ that was applied was a weighted average of all covariate models within 2 AICc units of the best-fit model. The inverse of $f(0,\boldsymbol{c}_j)$ is the effective strip width (ESW), which is the distance from the trackline beyond which as many sightings were made as were missed within.

Barlow (2006) used estimates of $g(0)$ adapted from previous studies of delphinids and large whales (Barlow, 1995), sperm whales (Barlow and Sexton[2]), and beaked whales and *Kogia* spp. (Barlow, 1999). However, results from recent work in which $g(0)$ was derived from apparent densities in different Beaufort sea state conditions (assuming that true density is not affected by sea state) indicate that $g(0)$ had been previously overestimated, particularly for high sea states (Barlow, 2015). Barlow (2015) estimated $g(0)$ in Beaufort sea states 0–6 for 20 cetacean taxa by using a model that accounted for spatial and temporal differences in density. This model was fitted to cetacean sighting data from the eastern Pacific, which included the on-effort sightings from the HICEAS in 2010. Therefore, the resulting estimates of $g(0)$ can be applied to the estimation of cetacean abundance for the HICEAS in 2010.

The estimates of $g(0)$ by Barlow (2015) were relative to a value of 1 at a Beaufort sea state of 0 for most species or species groups considered, with the exception of the Cuvier's beaked whale (*Ziphius cavirostris*) and *Mesoplodon* spp., for which scaled absolute estimates of $g(0)$ were determined for Beaufort sea states 0–6. In the absence of absolute estimates of $g(0)$ for most of the remaining taxa, the relative values of $g(0)$ from Barlow (2015) were assumed to be absolute values in the present study. Estimates of $g(0)$ for the HICEAS in 2010 (Table 3) were obtained by taking a weighted average of both the Beaufort-specific values of $g(0)$ and the associated coefficients of variation (CVs) presented in Barlow (2015), where the weights were the proportion of systematic effort in each sea state category (0–6) during the HICEAS in 2010.

For species not covered in Barlow (2015) because of small sample sizes, $g(0)$ was assumed to be similar to the $g(0)$ estimates of associated species in the species pools formed to model the detection functions, given the similar detection characteristics (e.g., size, surface behavior, group sizes) of the species in each pool (Table 2). Therefore, $g(0)$ for these species was obtained either by using the estimate of another species in the species pool or, if more than one estimate was available, by averaging the available estimates. Specifically, for the HICEAS in 2010, the estimate of $g(0)$ for striped dolphins (*Stenella coeruleoalba*) was used for Fraser's dolphins (*Lagenodelphis hosei*) and melon-headed whales (*Peponocephala electra*), the estimate for short-finned pilot whales was used for Longman's beaked whales (*Indopacetus pacificus*), and the estimates for rough-toothed dolphins (*Steno bredanensis*), bottlenose dolphins (*Tursiops truncatus*), and Risso's dolphins (*Grampus griseus*) were averaged for pygmy killer whales (Table 3).

The abundance of each species was determined by multiplying the density estimate by 2,447,635 km^2—the area of the Hawaiian Islands EEZ minus the area of the land masses of the main and Northwestern Hawaiian Islands. However, the ranges of the pelagic stocks of pantropical spotted and bottlenose dolphins, which are the stocks involved in the estimation (Table 1), do not span the entirety of the Hawaiian Islands EEZ (Carretta et al., 2011, 2014). Therefore, the area of the ranges of island-associated stocks of pantropical spotted and bottlenose dolphins was subtracted from the larger area, resulting in areas of 2,392,576 km^2 and 2,425,900 km^2 for pantropical spotted and bottlenose dolphins, respectively. The mixed parametric and nonparametric bootstrap routine described in Barlow (2006) and refined by Barlow and Rankin[3] was used

[2] Barlow, J., and S. Sexton. 1996. The effect of diving and searching behavior on the probability of detecting track-line groups, g_0, of long-diving whales during line-transect surveys. Southwest Fish. Sci. Cent. Admin. Rep. LJ-96-14, 21 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, 8901 La Jolla Shores Dr., La Jolla, CA 92037.]

[3] Barlow, J., and S. Rankin. 2007. False killer whale abun-

Table 3

Estimates of abundance and associated parameters for cetacean species and taxonomic categories sighted by observers on systematic effort during the Hawaiian Islands Cetacean and Ecosystem Assessment Survey within the U.S. Hawaiian Islands Exclusive Economic Zone in 2010. Mean group size (GS) is the average estimated GS (calibrated and proportioned to species; see text) of the sightings used in the abundance estimation (N_{EST} in Table 1). Mean effective strip width (ESW) is the average ESW of the N_{EST} sightings (computed from the covariates associated with each sighting) and represents the distance (in kilometers) from the trackline beyond which as many sightings were made as were missed within. As described in the text, probabilities of detection on the trackline ($g(0)$) were derived from Barlow (2015); coefficients of variation (CV) for $g(0)$ estimates are included in parentheses. The values in the CV column apply to estimates of both density, measured as individuals per 1000 km^2, and abundance. Log-normal 95% confidence intervals (CIs) for the abundance estimates are also shown.

Species or category	Mean GS	Mean ESW	$g(0)$ (CV)	Density	Abundance	CV	95% CI
Pantropical spotted dolphin	43.2	2.05	0.28 (0.07)	23.32	55,795	0.40	26,355 to 118,123
Striped dolphin	52.6	3.61	0.33 (0.07)	25.00	61,201	0.38	29,991 to 124,890
Rough-toothed dolphin	25.3	2.68	0.08 (0.21)	29.63	72,528	0.39	34,786 to 151,219
Bottlenose dolphin	33.5	2.46	0.27 (0.14)	8.99	21,815	0.57	7673 to 62,023
Risso's dolphin	26.6	2.53	0.58 (0.07)	4.74	11,613	0.43	5199 to 25,940
Fraser's dolphin	283.3	3.89	0.33 (0.07)	21.04	51,491	0.66	15,870 to 167,069
Melon-headed whale	153.0	4.06	0.33 (0.07)	3.54	8666	1.00	1693 to 44,372
Pygmy killer whale	25.7	2.28	0.31 (0.06)	4.35	10,640	0.53	4022 to 28,148
Short-finned pilot whale	40.9	2.88	0.60 (0.09)	7.97	19,503	0.49	7889 to 48,214
Killer whale	4.7	3.93	0.62 (0.26)	0.06	146	0.96	30 to 710
Sperm whale	7.4	4.42	0.64 (0.19)	1.86	4559	0.33	2450 to 8484
Blainville's beaked whale	7.0	2.29	0.11 (0.16)	0.86	2105	1.13	355 to 12,496
Cuvier's beaked whale	1.0	1.61	0.13 (0.16)	0.30	723	0.69	212 to 2471
Longman's beaked whale	59.8	2.97	0.60 (0.09)	3.11	7619	0.66	2348 to 24,723
Unidentified *Mesoplodon*	2.2	1.87	0.11 (0.16)	1.89	4624	0.48	1890 to 11,314
Unidentified beaked whale	3.1	1.95	0.12 (0.12)	1.17	2852	0.74	783 to 10,393
Bryde's whale	1.4	2.88	0.41 (0.12)	0.72	1751	0.29	1010 to 3035
Sei whale	3.1	2.85	0.41 (0.12)	0.16	391	0.90	87 to 1764
Fin whale	2.0	2.90	0.34 (0.17)	0.06	154	1.05	28 to 831
Blue whale	2.8	2.90	0.55 (0.21)	0.05	133	1.09	24 to 752
Sei or Bryde's whale	1.5	2.95	0.41 (0.12)	0.31	766	0.47	320 to 1833
Unidentified rorqual	1.6	4.04	0.43 (0.11)	0.17	423	0.46	180 to 991
Unidentified dolphin	15.2	3.31	0.36 (0.04)	5.82	14,241	0.33	7572 to 26,782
Unidentified cetacean	2.0	2.73	1.00 (N/A)	0.23	554	0.51	216 to 1421

(n=1000 iterations) to estimate the CV for each abundance estimate. Survey effort from all years (1986–2010) was divided into 150-km effort segments (the distance generally surveyed in 1 day). The bootstrap randomly sampled these effort segments with replacement and accounted for the variance associated with sampling variation, modeling the detection function (including model selection and averaging), and uncertainty in the estimate of $g(0)$. Following Barlow (2006), uncertainty in $g(0)$ was estimated by modeling $g(0)$ as a random normal deviate (logit-transformed) with a mean and variance chosen to provide the estimated $g(0)$ and CV used in the present study (Table 3).

Abundances were not estimated for seasonally migrating species of baleen whales and for most categories of unidentified cetaceans (i.e., not identified to species) sighted during the HICEAS in 2002 (Barlow, 2006). For the HICEAS in 2010, abundance estimates were determined for all species of baleen whales sighted while the observers were on systematic effort, with the exception of the humpback whale because the nearshore breeding range of this species was not representatively sampled during the survey. However, recent mark-recapture abundance estimates exist for humpback whales in the North Pacific (Barlow et al., 2011b), including the portion of the stock that overwinters in Hawaii waters (Allen and Angliss, 2014).

For completeness, the abundance of unidentified cetaceans encountered during the HICEAS in 2010 was also estimated. Specifically, abundance estimates were produced for unidentified *Mesoplodon* beaked whales; unidentified beaked whales; rorquals identified as either sei (*Balaenoptera borealis*) or Bryde's (*B. edeni*) whales; unidentified rorquals; unidentified small, medium, and large dolphins; unidentified dolphins; un-

dance and density: preliminary estimates for the PICEAS study area south of Hawaii and new estimates for the U.S. EEZ around Hawaii. Southwest Fish. Sci. Cent. Admin. Rep. LJ-07-02, 15 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, 8901 La Jolla Shores Dr., La Jolla, CA 92037.]

identified small and large whales; unidentified whales; and unidentified cetaceans (Table 1). Sightings of unidentified *Mesoplodon* beaked whales, unidentified beaked whales, and rorquals identified as either sei or Bryde's whales were pooled with associated species for modeling the detection function (Table 2). Sightings of unidentified small, medium, and large dolphins and unidentified dolphins were combined into a single category, "unidentified dolphins," for detection function and abundance estimation. Likewise, sightings of unidentified small and large whales and unidentified whales and cetaceans were combined into the category "unidentified cetaceans."

The detection functions for unidentified rorquals, "unidentified dolphins," and "unidentified cetaceans" were estimated separately and without testing for the effect of *species*. The $g(0)$ estimate for unidentified beaked whales was an average of the estimates for Cuvier's beaked whales and *Mesoplodon* spp.; the $g(0)$ estimate of unidentified rorquals was an average of the estimates for fin whales, blue whales, and sei or Bryde's whales; and the $g(0)$ estimate of "unidentified dolphins" was an average of the estimates for pantropical spotted, striped, rough-toothed, bottlenose, and Risso's dolphins and short-finned pilot whales (Table 3). A $g(0)$ estimate was not applied to the "unidentified cetaceans" because an appropriate value could not be determined, given the broad taxonomic range of this category.

Results

Survey sightings

During the HICEAS in 2010, the systematic and nonsystematic visual search effort spanned 20,568 km of transect lines in Beaufort sea states 0–6 within the Hawaiian Islands EEZ. During this effort and while off-effort, the observers sighted 379 cetacean groups (n=198 during systematic effort, n=101 during nonsystematic effort, n=80 during off-effort), which include 13 groups with more than one species present. Accounting for these mixed-species groups, the 379 group sightings represent 398 sightings of 23 species (17 odontocetes and 6 mysticetes) and 13 unidentified species categories (Table 1). With the exception of the pygmy sperm whale (*Kogia breviceps*) and the extremely rare North Pacific right whale (*Eubalaena japonica*), all cetacean species known to occur in the Hawaiian Islands EEZ were sighted during the HICEAS in 2010.

The systematic effort that was relevant to the abundance estimation encompassed 16,145 km of transect lines in Beaufort sea states 0–6 for most cetaceans sighted (Fig. 1), but for pantropical spotted and bottlenose dolphins, the effort covered 15,747 km and 16,100 km, respectively. As with the HICEAS in 2002 (Barlow, 2006), windy conditions prevailed during the HICEAS in 2010, and most (94.5%) of the systematic effort occurred in Beaufort sea states 3–6. Adjusting for mixed-species groups (n=9), the 198 groups sighted on systematic effort correspond to 211 sightings of 20 species and 11 unidentified species categories (Table 1; Fig. 2). The 3 species not sighted by the observers while on systematic effort during the HICEAS in 2010 were the spinner dolphin, the dwarf sperm whale (*Kogia sima*), and the minke whale (*Balaenoptera acutorostrata*).

By using the 177 sightings within the respective analytical truncation distances (N_{EST} in Table 1), abundance was estimated for 19 cetacean species (15 odontocetes and 4 mysticetes; see the *Materials and methods* section for the rationale for excluding humpback whales) and for the 11 unidentified species categories, although the latter were combined into 6 taxonomic categories (as described in the *Materials and methods* section). Of the 48 sightings of unidentified cetaceans used in the estimation of abundance, 9 sightings correspond with acoustic detections of dolphin whistles, odontocete clicks, or baleen whale calls. These detections were examined for possible insights into species identification. However, this effort did not lead to any gains in species identification because of either the poor quality of the recordings, the non-specificity of the vocalizations, or the confounding presence of an associated species.

Detection function

Of the 6 covariates of interest, only 4 (*Beaufort*, *group size*, *ship*, and *species*) were tested in the 10 models of detection function, although only the noncategorical covariates *Beaufort* and *group size* could be tested in all cases (Table 2). Insufficient samples sizes by *cruise number* and *year* prevented testing for the effect of these covariates on any of the detection functions. *Group size* and *Beaufort* most frequently contributed to the model-averaged estimates of detection function. Specifically, *group size* was selected in 6 detection functions and *Beaufort*, in 5 detection functions.

For the 7 detection functions in which *species* was a consideration, this covariate was tested in 3 cases and selected in 2 (Table 2). For the 4 species pools that had a limited sample size for testing the effect of *species*, follow-up modeling was performed in 3 cases to evaluate the potential for a *species* effect on the detection function. Specifically, for "species pool 1," a "striped dolphin" and "not striped dolphin" influence was examined. For "species pool 3," the evaluation was between "pilot whale" and "not pilot whale" sightings. For "species pool 5," the "other" sighting was excluded and a "Cuvier's beaked whale," "*Mesoplodon* spp.," and "unidentified beaked whale" effect was explored. By reducing the number of factor levels, *species* did enter 1 of the 4 acceptable models for the "species pool 5" detection function, but this covariate otherwise remained unselected for the 3 species pools. Follow-up modeling was not undertaken for "species pool 6" because there were not enough sightings to evaluate a "sei or Bryde's" and "not sei or Bryde's" effect. Overall, this post-hoc analysis of a *species* effect produced equivocal

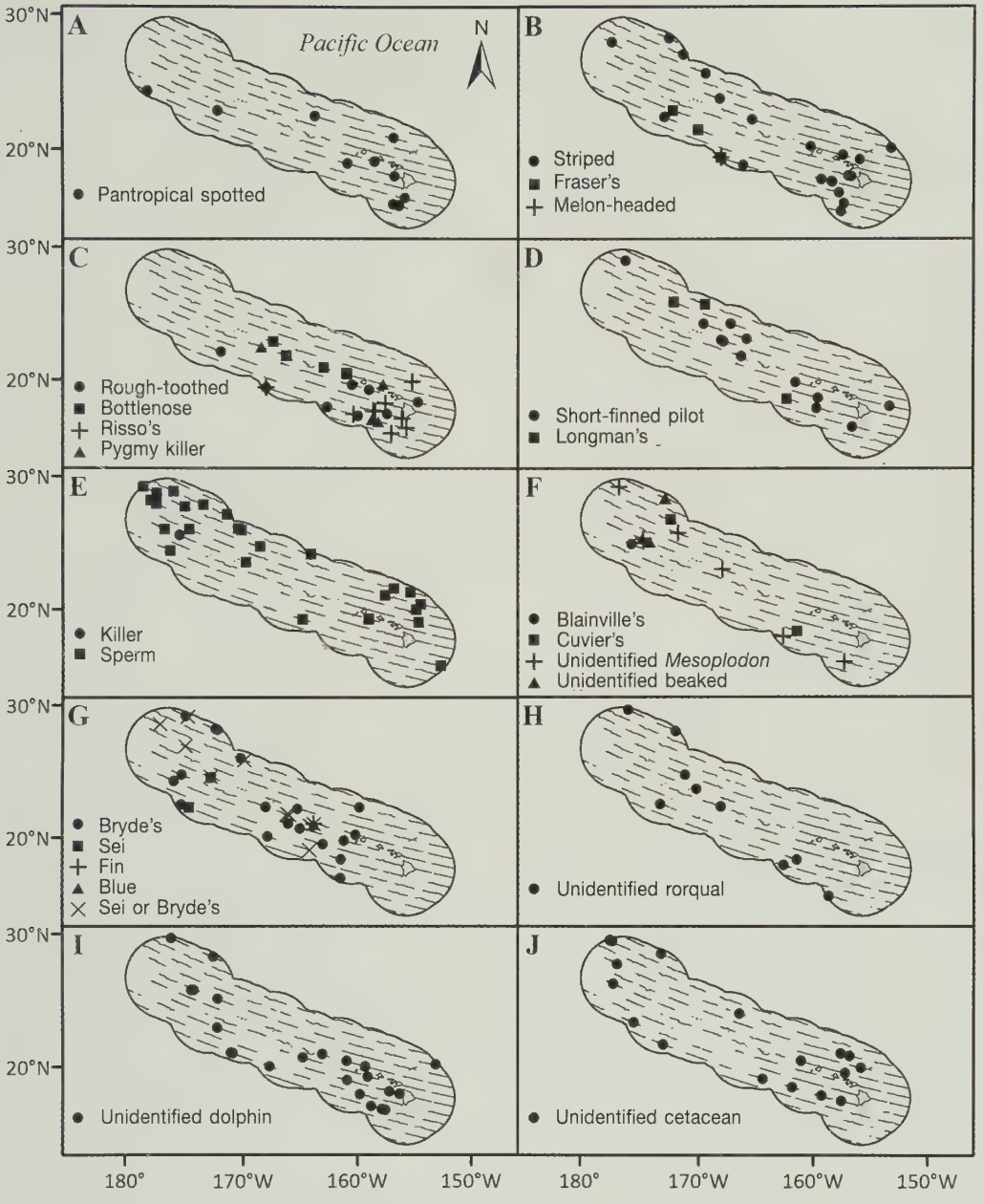

Figure 2

Sightings (N_{SYS} in Table 1; n=211) of cetacean species and taxonomic categories made by observers on systematic survey effort (fine lines) in Beaufort sea states 0–6 within the U.S. Hawaiian Islands Exclusive Economic Zone (thick black outline) during the Hawaiian Islands Cetacean and Ecosystem Assessment Survey in 2010. Sightings are grouped by detection function species pool (Table 2): (**A**) pantropical spotted dolphin, (**B**) species pool 1, (**C**) species pool 2, (**D**) species pool 3, (**E**) species pool 4, (**F**) species pool 5, (**G**) species pool 6, (**H**) unidentified rorqual, (**I**) unidentified dolphin, and (**J**) unidentified cetacean. The main Hawaiian Islands are shown in gray with a thin black outline.

results and, therefore, was not used in the abundance estimation.

Estimation of abundance

The mean group size and ESW of the sightings used in the estimation of abundance are shown in Table 3 for each species and taxonomic category. Mean group sizes range from 1.0 to 283.3 individuals and are highest for the small delphinids and lowest for the rorquals and beaked whales. One exception is the mean group size for the 3 sightings of Longman's beaked whales. At 59.8 individuals (range: 30.0–100.0 individuals), this mean group size is unexpectedly high given the mean group

size (10.1 individuals; range: 1.0–20.4 individuals) of all available sightings of Longman's beaked whales (n=9) made in the eastern Pacific by the SWFSC before 2010. Mean ESWs range from 1.61 to 4.42 km, are highest for the small delphinids (with the largest mean group sizes) and for killer and sperm whales, and are lowest for beaked whales (excluding Longman's beaked whales).

For most species sighted during the HICEAS in 2010, the proportions of systematic effort in Beaufort sea states 0–6 that were used to obtain survey-specific estimates of $g(0)$ from the values published in Barlow (2015) are 0.001, 0.012, 0.042, 0.122, 0.473, 0.304, and 0.046, respectively. The proportions used for pantropical spotted dolphins are 0.001, 0.012, 0.041, 0.124, 0.474, 0.301, and 0.046, and those used for bottlenose dolphins are 0.001, 0.012, 0.042, 0.122, 0.472, 0.303, and 0.046. The resulting estimates of $g(0)$ (Table 3) are substantially lower than those used in the estimation of abundance for the HICEAS in 2002 (Barlow, 2006, table 2).

Estimated densities of cetaceans by species and overall in the Hawaiian Islands EEZ during the HICEAS in 2010 are low (Table 3)—a finding that is consistent with results from the HICEAS conducted in 2002 (Barlow, 2006). Estimates of species density do not exceed approximately 30 individuals/1000 km^2, although more than half of the estimates are less than 2 individuals/ 1000 km^2. Accounting for the estimated density of false killer whales (Bradford et al., 2014, 2015), total cetacean density during the HICEAS in 2010 was approximately 146 individuals/1000 km^2. The most abundant species in the Hawaiian Islands EEZ during the summer–fall period of 2010 were the rough-toothed, striped, pantropical spotted, and Fraser's dolphins. The least abundant species were the blue whale (*Balaenoptera musculus*), killer whale, and fin whale (*B. physalus*). Approximately 4% of the estimated delphinid abundance represents unknown species, but more than 30% of the rorqual abundance and 40% of the beaked whale abundance could not be identified to species. The estimated abundance of cetaceans with unknown taxonomic status (i.e., "unidentified cetaceans") is relatively low. As expected, given the low number of sightings of most species, the CVs for the estimates of density and abundance are generally high.

Discussion

Although the HICEAS in 2010 was a follow-up survey to the HICEAS in 2002, comparisons between the data collected and the parameters estimated from the 2 surveys are complicated by several factors. At a basic level, there is random variation in the sampling process (e.g., survey conditions) and in the sighting attributes (e.g., group size) of the 2 surveys, and that variation can have a pronounced influence on the data and estimates, given the low sighting rates. For example, the mean group size of the 1 sighting of Longman's beaked whales made during the HICEAS in 2002 is 17.8 individuals (Barlow, 2006), compared with the mean of 59.8 individuals for the 3 sightings during the HICEAS in 2010. The single, chance sighting of 100 Longman's beaked whales in 2010 is alone a basis for expecting marked differences in the abundance estimates between the 2 surveys. In addition, although the total length of systematic survey effort during the HICEAS in 2010 (16,145 km) was similar to that of the HICEAS in 2002 (17,050 km), survey coverage within the pelagic portion of the Hawaiian Islands EEZ was somewhat greater in 2010 than in 2002 because 3350 km of the HICEAS in 2002 was dedicated to an intensive survey of the main Hawaiian Islands (Barlow, 2006). This shift in survey coverage along with random variation likely contributed to differences in the total number and species composition of sightings.

More broadly, there likely was interannual variation in oceanographic conditions between the 2 surveys that led to differences in the distribution and density of species in the study area (Forney et al., 2015). This factor becomes particularly important because the Hawaiian Islands EEZ is a jurisdictional rather than a biological stock boundary, and individuals from many associated stocks move into and out of the study area. Therefore, apparent differences in species stock density and abundance between the 2 surveys may not represent actual changes in the underlying population (or populations), but rather indicate a change in the proportion of the population within the Hawaiian Islands EEZ.

Finally, although data collection protocols were consistent and a similar analytical framework was used for each survey, differences in the estimation process make the resulting estimates difficult to compare. Although sightings from both the HICEAS in 2002 and 2010 were pooled with sightings from previous surveys for modeling detection functions, the pooled sightings for the 2010 estimation were limited geographically to minimize heterogeneity resulting from geographical differences in species associations and behavior and were further combined with sightings of species with similar detection characteristics. Differences in the pooled sightings used for modeling the detection functions likely partially explain differences in the estimates of mean ESW in 2002 and 2010 for many species (Barlow, 2006, table 3; Table 3).

However, the biggest difference in the estimation procedure for each survey is the use of the $g(0)$ estimates of Barlow (2015) in the analysis of data from the HICEAS in 2010. The present study is the first to apply these values to species in the central Pacific, and the resulting $g(0)$ estimates (Table 3) are markedly lower than those used by Barlow (2006), as well as those used in all known previous analyses of line-transect surveys of cetaceans. The $g(0)$ estimates in the present study reflect the effect of the sighting conditions during the HICEAS in 2010, represented by Beaufort sea state, and range from being 1.3 times (78.9%) smaller (i.e., for short-finned pilot whales and Longman's beaked whales) to almost 9 times (11.2%) smaller (i.e.,

for rough-toothed dolphins) than the $g(0)$ estimates of Barlow (2006). The estimates of $g(0)$ for 2010 are even more reduced than the values from 2002 for sightings with more than 20 individuals because $g(0)$ previously was assumed to be 1 for larger groups of most species (Barlow, 2006).

The lower $g(0)$ estimates for 2010, in combination with group sizes numbering in the tens to hundreds of individuals, are responsible for the relatively large estimates of abundance for the small and medium delphinids (Table 3)—values that are strikingly higher than the estimates determined by Barlow (2006). Point estimates of abundance in Barlow (2006) are larger than those of the present study for only 4 species: the killer and sperm whales, Blainville's beaked whale (*Mesoplodon densirostris*), and Cuvier's beaked whale. The estimates for killer and sperm whales are of the same magnitude in both studies and indicate that random variation in other aspects of the estimation (e.g., the number of encounters and group size for killer whales and the mean ESW for sperm whales) likely countered the effects of the slightly lower $g(0)$ estimates for the HICEAS in 2010.

The encounter rate for beaked whales was much lower for the HICEAS in 2010 because survey effort in Beaufort sea states 0–6 was used in the abundance estimation, but only effort in Beaufort sea states 0–2 was used in the analysis for the HICEAS in 2002 (Barlow, 2006). The corresponding decrease in $g(0)$ for the HICEAS in 2010 was not enough to reduce the effect of the decreased encounter rate for Cuvier's beaked whales, and random variation did not mitigate the effect, as the larger group size of the sighting in 2010 did for Blainville's beaked whales. As a result, the abundance estimate for Cuvier's beaked whales was more than 20 times larger for 2002 than for 2010. Results of an analysis in which habitat associations were used to estimate the densities and abundances of a subset of species encountered during the HICEAS in 2002 and 2010 (Forney et al., 2015) are also not directly comparable with results from the present study because Forney et al. (2015) used $g(0)$ estimates of the same order of magnitude as those in Barlow (2006).

A major assumption with cetacean line-transect analyses that was challenged by the estimation of $g(0)$ by Barlow (2015) is that $g(0)$ is equal to 1 for large groups of dolphins (Brandon et al.[4]; Gerrodette and Forcada, 2005). However, the model used to infer the relative values of $g(0)$ in different sighting conditions did not specifically test for the effect of group size on $g(0)$ or allow for potential interactions between group size and sighting conditions. The analysis did determine that group sizes decreased with increasing Beaufort sea state for many of the species considered (Barlow, 2015). If individuals of some species do form smaller groups in rougher sea conditions, abundance estimates based on observations of these groups would be positively biased. However, Barlow (2015) suggested that the decrease in group sizes at higher Beaufort sea states is more likely due to the underestimation of group size in rougher sea conditions.

Although more testing is needed, there is no evidence that actual group size changes as a function of Beaufort sea state (Barlow, 2015). Further, the Barlow (2015) $g(0)$ model not explicitly incorporating group size is presumably not an issue for the estimation in the present study unless the distribution of group sizes in the data subset from the HICEAS in 2010 is different from that of the full data set of the Barlow (2015) model. This question is difficult to assess qualitatively because summaries of mean group sizes from other study locales represented in the full data set (e.g., Ferguson et al., 2006; Barlow and Forney, 2007) do not reflect the underlying distribution of group sizes overall or by Beaufort sea state. Additional analyses are needed to quantitatively evaluate the effect of group size on the Beaufort-specific estimates of $g(0)$ and, therefore, to confirm that the estimates can be applied to all group sizes in the study locations covered by Barlow (2015). Validation of the actual $g(0)$ estimates (e.g., by comparisons with acoustic detections) would also be valuable.

For the species that were sighted during the HICEAS in 2010 (Table 3), but were not included in the analysis of Barlow (2015) (i.e., the Fraser's dolphin, melon-headed and pygmy killer whales, and Longman's beaked whale), use or averages of the $g(0)$ estimates of associated species in the detection function species pools (Table 2) may not have been appropriate and could have biased the estimation of abundance for these species. Future efforts to estimate $g(0)$ for these species when sufficient sample sizes are available would resolve this issue and are recommended.

The rough-toothed dolphin was noted as an outlier in the estimation of $g(0)$ by Barlow (2015), showing the most rapid decline in $g(0)$ with increasing Beaufort sea state of all the species. The impact of this effect is clear in the abundance estimation for the HICEAS in 2010 in that the value of $g(0)$ for the rough-toothed dolphin is the lowest of all the species and the resulting abundance estimate is the highest (Table 3). Given their relatively small group sizes and subtle surfacing behavior (i.e., surfacing without conspicuous splashes), rough-toothed dolphins have been described by experienced observers as difficult to detect (Yin[5]), but this characterization has not been explicitly quantified and is not readily apparent from qualitative comparisons of multispecies data. For example, the mean group size and ESW for rough-toothed dolphins in this study are

[4] Brandon, J., T. Gerrodette, W. Perryman, and K. Cramer. 2002. Responsive movement and g(0) for target species of research vessel surveys in the eastern tropical Pacific Ocean. Southwest Fish. Sci. Cent. Admin. Rep. LJ-02-02, 28 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, 8901 La Jolla Shores Dr., La Jolla, CA 92037.]

[5] Yin, S. 2015. Personal commun. Hawaii Marine Mammal Consortium, Kamuela, HI 96743.

not smaller than those of the other medium delphinids (Table 3).

In a multispecies assessment of odontocetes in Hawaii that was based on small-boat surveys, Baird et al. (2013) found that measures reflecting the detectability of rough-toothed dolphins (i.e., mean group size, mean distance when first sighted, and sightings per unit of effort) were nearly identical to those for bottlenose dolphins, and individuals of both species are frequently sighted around the main Hawaiian Islands. Resighting rates of individual rough-toothed dolphins were high enough to indicate that island-associated populations are not exceptionally large (Baird et al., 2008). The results from Baird et al. (2008) pertain to island-associated populations, but Barlow (2006) estimated that the density of rough-toothed dolphins was approximately 2.5 times higher within 140 km of the main Hawaiian Islands than throughout the rest of the Hawaiian Islands EEZ. Therefore, there are no available quantitative measures that would indicate that rough-toothed dolphins are particularly more difficult to see than individuals of other species or have especially high abundance in the Hawaiian Islands EEZ. Further, rough-toothed dolphins frequently associate with individuals of other species and are generally not known to avoid vessels (Baird et al., 2008). Hence, a source of negative bias in the $g(0)$ estimates of Barlow (2015) for rough-toothed dolphins is not obvious.

Rough-toothed dolphins were used as a case study in an evaluation of the use of passive acoustics as an independent detection platform for observers in the eastern tropical Pacific (Rankin et al.[6]). That study estimated that a majority of groups of rough-toothed dolphins were missed on the trackline. Because additional species were not assessed, it is unclear how often rough-toothed dolphins were missed in comparison with individuals of other species. Overall, the low $g(0)$ estimates and correspondingly high abundance estimates of rough-toothed dolphins in the Hawaiian Islands EEZ cannot be explained.

As with the abundance estimates from the HICEAS in 2002 (Barlow, 2006), the precision of the estimates from the HICEAS in 2010 is generally poor (Table 3). For both sets of estimates, this imprecision is largely a result of the low number of sightings of most species. That is, these low numbers of sightings led to a high variance in each encounter rate that dominated the overall CV estimate (Barlow, 2006). However, the CVs of most estimates of abundance for 2010 are lower than the estimates for 2002, despite the addition of covariate model selection and averaging in the bootstrap procedure used in the estimation for 2010. This slight increase in precision could be linked to the greater number of sightings during the HICEAS in 2010. Sample sizes for modeling the detection functions were generally higher in the analysis for 2002 because pooled sightings from throughout the eastern North Pacific were used (Barlow, 2006). Although restricting the assessment for 2010 to sightings from the central North Pacific reduced available sample sizes for the estimation of detection functions, it likely reduced heterogeneity that could not be accounted for by covariate testing and could have resulted in more precise abundance estimates for 2010.

Cetaceans were sighted throughout the Hawaiian Islands EEZ (Fig. 1), but the distributions of sightings, by species, indicate areas of concentration for some species (Fig. 2). For example, sightings of pantropical spotted dolphins were concentrated south of the main Hawaiian Islands, and sightings of sperm whales were concentrated in the northwestern portion of the Hawaiian Islands EEZ. The underlying distributions represent species-specific habitat associations and can vary temporally and spatially, leading to differences in species distributions between the HICEAS in 2002 and 2010 (Forney et al., 2015). These habitat associations were used to predict higher densities around the Hawaiian Archipelago for several species, although not for all of them (Forney et al., 2015).

Even with island-influenced productivity, the waters of the Hawaiian Islands EEZ are generally oligotrophic—a condition that is reflected in the low density of cetaceans in the Hawiian Islands EEZ compared with densities in areas with relatively high production (e.g., Wade and Gerrodette, 1993; Mullin and Fulling, 2004; Barlow and Forney, 2007). For example, total cetacean density in the eastern tropical Pacific was estimated to be 520 individuals/1000 km^2 (Wade and Gerrodette, 1993), and total cetacean density in the Southern California portion of the California Current ecosystem was estimated to be 678 individuals/1000 km^2 (calculated from values given in Barlow and Forney, 2007). Both of those studies underestimated abundance by overestimating $g(0)$. Despite the application of the lower Beaufort-specific values of $g(0)$ in the present study, total cetacean density was estimated to be only 146 individuals/1000 km^2.

Approximately 93% of the estimated cetacean density for the HICEAS in 2010 consists of dolphin species. On the basis of sighting frequencies from small-boat surveys, Baird et al. (2013) suggested that the pantropical spotted dolphin was the most abundant cetacean species around the main Hawaiian Islands. In the broader Hawaiian Islands EEZ, the pantropical spotted dolphin was the thirdmost abundant species after the rough-toothed and striped dolphins (Table 3). The density of large whales (i.e., sperm and baleen whales) during the HICEAS in 2010 was about 2% of the total estimated cetacean density. The sperm whale was estimated to be the most abundant large whale species in the Hawaiian Islands EEZ, although the estimated density of 1.86 individuals/1000 km^2 for this species is just over half the density of sperm whales in the northeastern

[6] Rankin, S., J. Barlow, J. Oswald, and T. Yack. 2009. A comparison of the density of delphinids during a combined visual and acoustic shipboard line-transect survey [Abstract]. *In* 1st international workshop on density estimation of marine mammals using passive acoustics; Pavia, Italy, 10–13 September, p. 75. [Available at website, accessed May 2015.]

temperate Pacific (Barlow and Taylor, 2005). However, the Barlow and Taylor (2005) density estimate of 3.38 individuals/1000 km^2 is based on a value of $g(0)$ that does not account for varying sighting conditions and, therefore, is likely to be an underestimate.

Density and abundance estimates of the seasonally migrating species of baleen whales (i.e., the sei, fin, and blue whales) are difficult to interpret because the HICEAS in 2010 was not conducted during the winter period of peak abundance for these species. However, the estimates do indicate the presence of individuals of these species in low numbers during the summer and fall (Table 3), as has been determined with acoustic studies of fin and blue whales (Thompson and Friedl, 1982). Bryde's whales remain year-round at tropical and subtropical latitudes and were estimated to have a density of 0.72 individuals/1000 km^2 during the HICEAS in 2010. This density is similar to the value of 0.68 individuals/1,000 km^2 in the eastern tropical Pacific (Wade and Gerrodette, 1993), although this value would presumably increase with the application of appropriate $g(0)$ estimates.

Beaked whales accounted for the remaining 5% of cetacean density in the Hawaiian Islands EEZ during the HICEAS in 2010. The densities of *Mesoplodon* spp. and Cuvier's beaked whales during the HICEAS in 2010 were estimated to be 2.75 and 0.30 individuals/1000 km^2, respectively—values that are lower than estimates of 2.96 and 4.55 individuals/1000 km^2 from the eastern tropical Pacific (Ferguson et al., 2006), particularly for Cuvier's beaked whales. Although only 4% of the estimated delphinid abundance in the HICEAS in 2010 could not be identified to species, more than 30% of the rorqual abundance and 40% of the beaked whale abundance could not be identified to species. In addition to the use of new acoustic information or updated g(0) values, future efforts to refine the abundance estimates for the HICEAS in 2010 could include the use of a proration approach (e.g., Wade and Gerrodette, 1993) to assign the abundance of unidentified rorquals and beaked whales to species.

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Use of gill nets and telemetry in tracking movements and feeding of striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) at a salinity front in a small estuary

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Abstract—The hypothesis that striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and species of forage fish would be associated closely with a salinity transition front was tested through sampling and tagging efforts. In a small New Jersey estuary, a station at a salinity front and another in a nearby channel were sampled weekly with gill nets. Abundance of bluefish was significantly greater at the front, and abundance of weakfish was significantly greater at the channel. Forage fish were collected at both stations, and the diets of bluefish and weakfish overlapped in all seasons. Ultrasonically tagged striped bass, weakfish, and bluefish were tracked concurrently, and their home ranges, or the 95% probability of their occurrences were computed. Home ranges of tagged striped bass occurred upriver and also near river kilometer 1. Home ranges of weakfish were located in the midriver channels, and those of bluefish were located midriver and upriver at river kilometers 5–12. Home ranges for these 3 species were not limited to the area of the salinity front, contrary to the initial hypothesis.

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Small tributaries of temperate-zone estuaries have vital but incompletely understood roles as sources of energy for growth of many sought-after commercial and recreational fish species. In flood-dominated estuaries, tidal movements and freshwater discharges create a salinity transition zone or front, where saline and riverine waters mix, with a salinity gradient forming both horizontally and vertically. Turbulent mixing in this zone may produce a turbidity maximum, where inorganic and organic particulates are suspended. The frontal boundary allows retention of nutrients, phytoplankton, microbes, and zooplankton (Grimes and Kingsford, 1996; Epifanio and Garvine, 2001). High freshwater discharges stabilize the duration and volume of such a nutrient-rich habitat (Morgan et al., 1997; Roman et al., 2001). It has been hypothesized that, with such mixing, food is concentrated for consumers, including larval and small-size fish, which in turn attract larger predators (North and Houde, 2001; Martino and Houde, 2010).

The Navesink River, a flood-dominated small tributary of the Hudson–Raritan Estuary in New Jersey that borders the Mid-Atlantic Bight, is used by predatory fish, forage fish, and invertebrate species (Shaheen et al., 2001; Stoner et al., 2001; Meise and Stehlik, 2003; Scharf et al., 2004; Manderson et al., 2006; Manderson et al.[1]). Previous hydrographic studies have delineated a convergence zone or salinity transition zone in the upper river (Chant and Stoner, 2001; Fugate and Chant, 2005). In this river system, 3 of the dominant pelagic predators are bluefish (*Pomatomus saltatrix*), striped bass

[1] Manderson, J. P., J. Pessutti, J. Rosendale, and B. Phelan. 2007. Estuarine habitat dynamics and telemetered movements of three pelagic fishes: scale, complexity, behavioral flexibility and the development of an ecophysiological framework. ICES Council Meeting (C.M.) Documents 2007/G:02, 36 p.

(*Morone saxatilis*), and weakfish (*Cynoscion regalis*). In estuaries, these 3 species are predators of fish and invertebrate species in varying proportions depending on season and availability (Lankford and Targett, 1994; Buckel and Conover, 1997; Collette and Klein-MacPhee, 2002; Nemerson and Able, 2004; Rudershausen et al., 2005; Ferry and Mather, 2012). They are frequently sympatric and are competitors for the same prey (Hartman and Brandt, 1995; Uphoff, 2003). In a study in which gill nets were used in the Navesink River in 1998 and 1999 (Scharf et al., 2004), abundance of bluefish was greatest at a station in the upper river in the Red Bank basin and was significantly correlated with areas of fine sediment.

From May through October in 2006 and 2007, Manderson et al. (2014) conducted a weekly hydrographic study of the Navesink River from river kilometers 1–12. On 12 of those weeks, they also conducted a hydrographic study limited to the area around the salinity front in the upper or western end of the river, together with fish collection and diet analysis. Concurrently, acoustically tagged bluefish (age 0 and age 1+), weakfish, and striped bass were monitored by using receivers throughout the river to determine days of continuous occupation and movements by individuals of these 3 species (Manderson et al., 2014). Median residence times in 2007 were 8 d for striped bass, 29 d for age-1+ bluefish, 29 d for age-0 bluefish, and 47 d for weakfish. Manderson et al. (2014) concluded that the seasonal residencies of these predators in the Navesink River were affected by 2 direct factors: variation in day length and temperature. Freshwater discharge also affected predator residence times indirectly, possibly through prey availability (Manderson et al., 2014).

On the basis of the analyses reported in Manderson et al. (2014), we hypothesized that, when freshwater discharge was moderate to high, biophysical mechanisms supporting the salinity transition zone and concentrating food resources would be maintained and predators would chiefly reside there. We hypothesized that, when discharge was low, the salinity transition zone would be disrupted, resulting in a reduction in food resources and emigration of predators from the zone or the entire estuary. Manderson et al. (2014) did not examine evidence extensively for testing this hypothesis, including examining within-estuary movements of predators, occurrence and distributions of prey, and diets, or the potential relationship of the biota to hydrographic features in the estuary.

The objective for this study was to test the hypothesis that striped bass, bluefish, and weakfish are more abundant in the vicinity of the main salinity transition zone or front of the Navesink River than away from it. We used data from hydrographic surveys, gill net collections, predator diets, and telemetry to evaluate the available evidence that supports or disproves our hypothesis. The telemetry data were used to generate daily and composite home ranges of the 3 predator species in this river.

Materials and methods

Study area

The Navesink River is approximately 12 km long, ≤1.5 km wide, and around 10 km^2 in area (Fig. 1); it flows eastward into the Shrewsbury River, then north to Sandy Hook Bay and Raritan Bay. It is a flood-dominated estuary, with a 1.4-m average tidal range (Chant and Stoner, 2001). The salinity front is near this upper or western end of the river (Fugate and Chant, 2005), and practical salinity ranges from ~1 in the upper Navesink River during spring freshets to ~28 at the mouth of this river (senior author and J. Manderson, unpubl. data). To the west, the Swimming River is the primary freshwater source. The upper river depth for the Navesink River averages ~2 m at high tide, and substrates are fine sand and silt with high organic content (Chant and Stoner, 2001; Stoner et al., 2001; Meise and Stehlik, 2003). The lower Navesink River is characterized by shallow sandbars and channels (depths up to 4 m). High-velocity tidal currents and coarse to medium sands are found in the channels. Shallows and embayments in the summer and fall are vegetated with sea lettuce (*Ulva lactuca*) and other macroalgae. For our studies, we designated the confluence of the Navesink and the Shrewsbury rivers as river kilometer 0.

Hydrographic measurements and station locations

Weekly hydrographic surveys were made the length of the river from April through October, in 2007, along transects that intersected with an array of ultrasonic receivers (see *Telemetry* section). An SBE 25 Sealogger[2] conductivity, temperature, and depth recorder (Sea-Bird Electronics Inc., Bellevue, WA) was cast at the location of each receiver, to measure temperature, conductivity, pressure, dissolved oxygen, photosynthetically active radiation, turbidity, and concentration of chlorophyll-*a*. Similar work was completed in 2006 with the same equipment and methods (see Manderson et al.[1]).

Hydrographic mapping and gill net sampling at the upstream end of the Navesink River, near the salinity front, were conducted during 12 weeks in May through October 2007. Hydrographic mapping took place twice a day during daylight hours at the end of flood and at the end of ebb tides, once a week on 4 consecutive weeks during each of 3 periods: spring (May), summer (late July–early August), and fall (late September–early October). We integrated data from a global positioning system (GPS), the SBE 25 Sealogger, and a Hydrolab datasonde (OTT Hydromet, Kempten, Germany) that measured temperature and salinity at 1-s intervals 0.5 m below the surface. After the salinity front was located by using the SBE 25 Sealogger, the site of

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

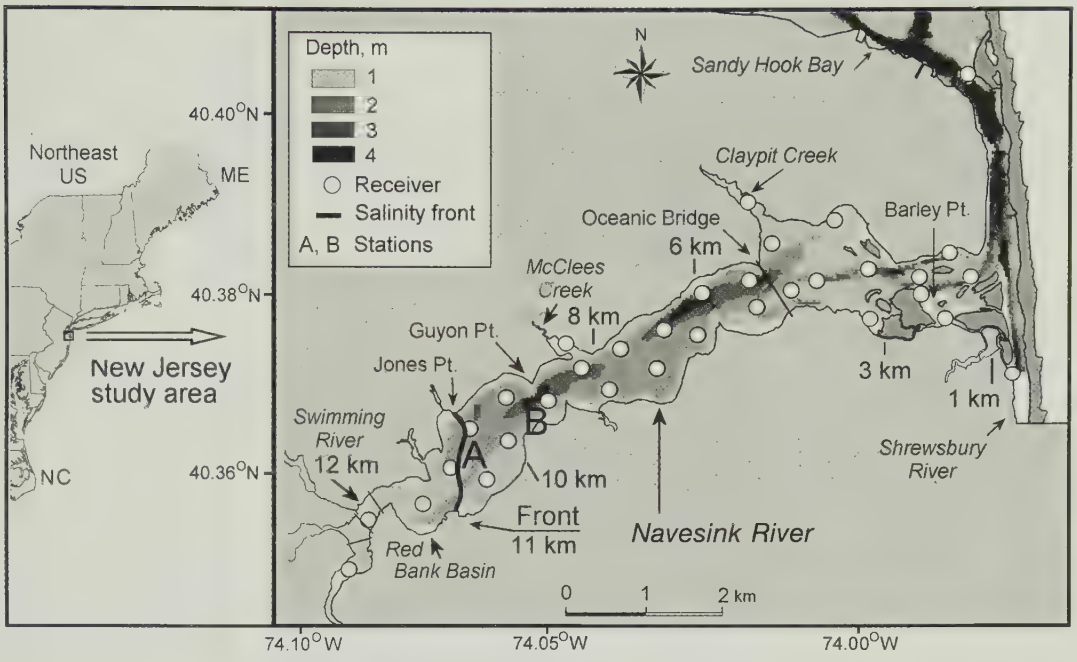

Figure 1

Map of the Navesink River, showing the location of the river on the northeastern coast of the United States, depths at mean low low water, locations of receivers used to track ultrasonically tagged bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), and weakfish (*Cynoscion regalis*) in 2007 (indicated with circles), approximate location of the salinity transition front at flood tide (indicated by the black line) in 2007, and locations of station A at the front at flood tide and station B at a nearby channel, where gill net sampling was conducted in 2007 (indicated with the letter A or B).

that cast of the SBE 25 where the front was found was designated as station A (depth: 1–2 m at low tide) for gill net sampling. The location of station A changed depending on the hydrodynamics. When the tide changed that day, station A was relocated. Station B for gill net sampling was located approximately 2 km downriver in a nearby channel (depth: 3–7 m at low tide) and was always in the same location (Fig. 1).

Freshwater discharge records were obtained from U.S. Geological Survey streamflow station 01407500 in the Swimming River west of Red Bank, New Jersey (data available at website; Manderson et al., 2014).

Fish collections and diets

To investigate predator diets and prey distributions, we used targeted gill net sampling during the 12 weeks of hydrographic surveys. Three replicate nets were deployed at each of the stations A and B, at peak of flood tide and at peak of ebb tide, twice daily. They were anchored close to the river bottom, and were soaked for 2 h in the morning and again in the afternoon of that same day. The gear and soak times were chosen to be the same as those employed in 1998 and 1999 by Scharf et al. (2004). Gill nets were 45.7 m in length by 2.4 m depth, had 6 panels of equal length (7.6 m) and various mesh sizes (1.3–7.6 cm^2). After fishing for 2 h, gill nets were retrieved. Fish and macroinvertebrates captured in each net were sorted, counted, and measured. Striped bass and weakfish were measured in total length (TL), and measurements of bluefish were taken in fork length and converted to TL. Weakfish and bluefish were assigned to either age-0 or age-1+ (age 1 or older) cohorts on the basis of analysis of length frequencies in the earlier study (Scharf et al., 2004). Weakfish and bluefish <300 mm TL in spring and fall and <250 mm TL in summer were classified as age-0. Relative abundances of fish species from the front and channel stations were compared by using Mann-Whitney tests ($P<0.05$).

Stomachs of the targeted predators were removed and preserved in 70% ethanol. Stomachs <5% full and those containing only unidentified matter were counted as empty. Fish and invertebrate prey were identified to the lowest possible taxonomic level, weighed wet (to the nearest 0.01 g), and lengths (in millimeters) of intact prey items were recorded. The most important prey taxa by percent weight of all predators were pooled into 10 categories, including a category for unidentified fish or other organisms. Cluster analysis was performed by the least squares method on percentages of prey taxa by predator, age class, and season. However, too few striped bass were collected to conduct any diet analysis.

Gill net collections were used to identify typical distributions of dominant prey taxa. We chose the size limit for predator-vulnerable fish as ≤150 mm TL, on the basis of lengths of prey in stomach contents from

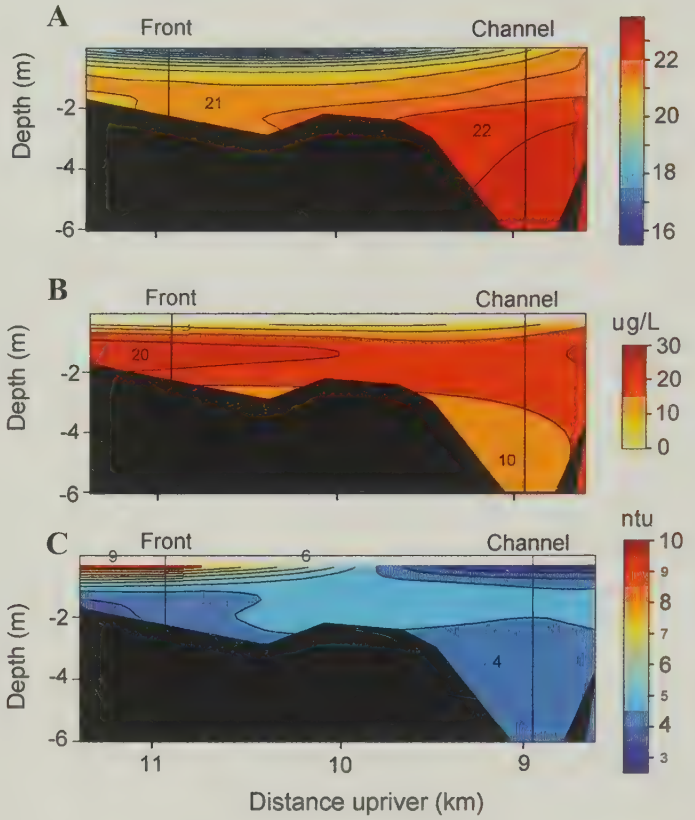

Figure 2

Hydrographic profiles of (**A**) salinity, (**B**) chlorophyll-*a* concentration (µg/L), and (**C**) turbidity (ntu) in the upper Navesink River, in New Jersey, at flood tide on 2 August 2007. Locations of station A at the salinity transition front and station B at a nearby channel that were sampled with gill nets are marked.

the study in 1998 and 1999 (senior author and J. Manderson, unpubl. data). In the field of potential prey, we included bay anchovy (*Anchoa mitchilli*, 50–110 mm TL), Atlantic silverside (*Menidia menidia,* 60–130 mm TL), and Atlantic menhaden (*Brevoortia tyrannus*, 50–150 mm TL), as well as bluefish and weakfish ≤150 mm TL.

Telemetry

Ultrasonic telemetry was used in 2006 and 2007 to monitor the movements of bluefish, weakfish, and striped bass by using methods described in detail by Manderson et al. (2014). Briefly, we moored an array of omnidirectional receivers (model VR2, Vemco, Bedford, Nova Scotia, Canada) ~80 cm above the bottom throughout the Navesink River from 15 May through 3 October 2006 and from 18 April through 31 October 2007. In 2006, the array consisted of 27 receivers. In 2007, 5 additional receivers were moored in marsh creeks and coves. Nearest neighbor distances between receivers in the river averaged 493 m (standard deviation 141 m), within a range of 216–788 m. Receivers moored in the middle and upper river had detection ranges of 350–600 m, whereas detection ranges were smaller and more variable in the topographically complex lower river (details of range tests are provided in Manderson et al., 2014).

From 14 May through 8 September 2006 and from 1 May through 2 October 2007, striped bass, bluefish, and weakfish were caught by hook and line when seasonally available. They were placed in coolers with cooled water from the laboratory and with battery-operated airstones and were transported within 1 h to the laboratory. Fish were anaesthetized with AquiS (AquiS New Zealand Ltd., Lower Hutt, New Zealand) at a concentration of 54 mg/L. A sterilized, uniquely coded ultrasonic transmitter (V9-6L, Vemco), with a frequency of 69 kHz and a repetition rate of 40–120 s, was then inserted into the body cavity of each fish. Fish were held in the laboratory 2–48 h afterward so that we could be certain of their recovery and were

Table 1

Total catch of striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) by season, age class, and station (located at a channel [B] or salinity transition front [A]) for gill net sampling conducted in the Navesink River, New Jersey, in 2007.

Species and age class	Spring Channel	Spring Front	Summer Channel	Summer Front	Fall Channel	Fall Front
Age-1+ striped bass	1	6	0	0	0	0
Age-0 bluefish	0	0	46	86	147	389
Age-1+ bluefish	1	5	21	0	3	0
Age-0 weakfish	0	0	94	4	261	52
Age-1+ weakfish	88	3	53	7	31	7

then released randomly throughout the river. In 2006, 34 age-1+ striped bass (359–630 mm TL), 14 age-1+ bluefish (310–390 mm TL), 15 age-0 bluefish (175–270 mm TL), and 15 age-1+ weakfish (224–535 mm TL) were released. In 2007, 12 age-1+ striped bass (342–510 mm TL), 21 age-1+ bluefish (310–610 mm TL), 30 age-0 bluefish (222–275 mm TL), and 27 age-1+ weakfish (304–480 mm TL) were released.

The home range of an animal, where it spends 95% of its time during normal activities, was calculated for each species by using the "utilization distribution" method (Anderson, 1982; Tolimieri et al., 2009). Those fish that were ultrasonically detected 3 or more times on a given day and that were detected on a minimum of 6 days were included in our analysis. The adehabitatHR package (Calenge, 2006) in R, vers. 2.13.1 (R Core Team, 2011) was used to perform the analysis on the telemetry records. Signals were binned in 10-min intervals. Records were censored in instances when signals from more than one fish overlapped in a time bin. Because the Navesink River is relatively narrow in relation to the detection range of the receivers used in this study, mean daily positions in universal transverse coordinates were converted to distances upriver (in meters). Home ranges were generated for individual fish by using an analysis grid of squares with sides 100 m×100 m, limited to areas within the coastline boundary. Composite grids for all data from each species were then generated and plotted for each species, age class (in bluefish), and year.

Results

Hydrography

When freshwater discharge was high, a well-defined salinity gradient was established in the upper Navesink River. At end of flood tide, this gradient was located at approximately river kilometers 10–11 between Jones Point and just east of the basin off Red Bank (Fig. 1). Usually, the salinity front shifted 0.5–1.5 km downstream with ebb tide. In 2007, freshwater discharge was high although variable in July and August, and discharge was low in September and October (Manderson et al., 2014), leading to a fully mixed salinity state in the river in fall.

In a hydrographic profile of the upper portion of the Navesink River on 2 August 2007, during a period of high freshwater discharge, the salinity gradient was from near 17 at the surface to >22 near the channel bottom, at both tides (Fig. 2). The salinity front at high tide was located at the steepest vertical salinity gradient at approximately river kilometer 11. The surface layer in the upper river at that time was 25.5°C and contained concentrations of chlorophyll-*a* >20 µg/L, at approximately river kilometers 7–11. West of the front near the surface was a zone of high turbidity, an area that typically extended into the Swimming River.

In contrast, at a time of low discharge in late September and October 2007, the estuary was well mixed and hydrographic profiles were much more uniform. No clearly delineated front was observed. The differences between the units of the contours of salinity and chlorophyll-*a* concentration in the upper river profiles were one-tenth the magnitude of the differences between the units in August, and turbidity was high only in the Swimming River.

Predators, predator diets, and prey field

During gill net sampling, 7 age-1+ striped bass, 30 age-1+ bluefish, 648 age-0 bluefish, 189 age-1 weakfish, and 411 age-0 weakfish were collected (Table 1). The seasonal arrival and egress of the species were discussed by Manderson et al. (2014). Catch at station A at the salinity front, as opposed to station B in the channel, was significantly different for all taxa and seasons (Mann-Whitney tests: $P<0.01$). Almost twice as many age-0 bluefish were collected at the front station than at the channel station in summer and fall. Age-1+ bluefish were collected rarely except in summer, and during

Table 2

Categories of most important prey found in stomach contents of bluefish (*Pomatomus saltatrix*) and weakfish (*Cynoscion regalis*) captured during gill net sampling in 2007 in the Navesink River, New Jersey, expressed by season and age class as a percentage of total weight.

Species	Bluefish	Bluefish	Bluefish	Weakfish	Weakfish	Weakfish	Weakfish	Weakfish
Season	Summer	Summer	Fall	Spring	Summer	Summer	Fall	Fall
Age class	Age-0	Age-1+	Age-0	Age-1+	Age-0	Age-1+	Age-0	Age-1+
N	73	18	259	70	17	42	127	22
Amphipoda	0.11	0.00	0.00	0.02	28.27	0.00	4.27	0.00
Mysidacea	0.00	0.00	0.00	41.00	0.13	0.01	0.00	0.00
Caridea	4.29	0.77	0.03	56.67	17.38	3.56	3.89	0.00
Brachyura	15.83	72.75	0.29	2.02	0.00	22.27	2.64	0.47
Anchoa mitchilli	1.41	0.00	0.57	0.00	4.54	0.00	0.65	0.00
Brevoortia tyrannus	47.41	1.18	94.67	0.00	40.99	32.04	83.39	95.85
Cynoscion regalis	5.02	0.00	0.00	0.00	0.00	6.70	0.00	0.00
Menidia menidia	8.31	2.51	1.34	0.00	0.00	3.86	1.04	0.00
Pomatomus saltatrix	0.00	12.75	0.00	0.00	0.00	2.55	0.00	0.00
Fish, unid. and other organisms	17.62	10.04	3.09	0.30	8.69	29.01	4.13	3.72

that season they were captured largely in the channel. Age-0 and age-1+ weakfish were more abundant at the channel station than at the front station in all seasons.

Overall, the most important prey by percent weight was Atlantic menhaden (Table 2). By cluster analysis (at 30% similarity), the greatest differences in diet resulted with season and age class, and with predator species of lesser importance. In spring, age-1+ weakfish consumed mainly sand shrimp (*Crangon septemspinosa*) and mysids (*Neomysis americana*). In summer, age-0 bluefish, median length 150 mm TL, ate age-0 Atlantic menhaden, species of the infraorder Brachyura, Atlantic silverside (*Menidia menidia*), age-0 weakfish, and other fish species. In that season, age-1 bluefish ate species of Brachyura (mainly blue crabs [*Callinectes sapidus*]) and smaller bluefish. In summer, weakfish consumed Atlantic menhaden, other fish species, and blue crabs, and the age-0 weakfish also consumed amphipods and species of the infraorder Caridea (sand shrimp and grass shrimp [*Palaemonetes* spp.]). The other fish species in both seasons included winter flounder (*Pleuronectes americanus*) and striped searobin (*Prionotus evolans*). In fall, Atlantic menhaden constituted 91.9% of the stomach contents of all predators at both stations.

Differences in stomach contents between stations A (front) and B (channel) were found only for bluefish in summer. At that time, bluefish consumed more crabs at station B than at station A and more Atlantic menhaden at station A than at station B (Mann-Whitney tests: $P<0.01$).

Potential prey fish were captured in the fine mesh panels of the gill nets at both Stations A and B (Fig. 3). Summer was the only season in which the catch at the 2 stations was different. At that time, significantly more Atlantic silverside were caught at the front than at the channel, and significantly more Atlantic menhaden were captured at the channel than at the front (Mann-Whitney tests: $P<0.01$). In summer, age-0 bluefish and weakfish were also potential prey, the former at the front and the latter at the channel. In fall, nearly all the potential prey collected at both stations were age-0 Atlantic menhaden. Although bay anchovy were common in predator diets, they were rarely collected in the gear during sampling.

Telemetry

Home ranges for ultrasonically tracked striped bass, bluefish, and weakfish in the Navesink River in 2006 and 2007 averaged 73–133 m^2 in area, depending on species (Table 3). There was great variation among individuals of each taxon. Striped bass had the smallest home ranges by area. Home ranges of age-1+ bluefish were larger than those of weakfish and age-0 bluefish, although not significantly different.

From 2006 through 2007, 89 tracked fish met the criteria for mapping, and the centers of their home ranges were located mainly in one or more of 4 defined reaches of the estuary (Figs. 4 and 5). Detections were relatively few in number at river kilometers 3–5 and 7–8.

Reach 1 Shoals and islands in the lower river near the confluence of the Navesink and Shrewsbury rivers (river kilometers 1–3).

Reach 2 Channel on both sides of the Oceanic Bridge (river kilometers 5–7).

Reach 3 From McClees Creek to the channels off Guyon Point, including Station B (river kilometers 8–10).

Reach 4 Upper river, from the Red Bank basin to Jones Point, including the salinity front and Station A (river kilometers 10.0–11.5).

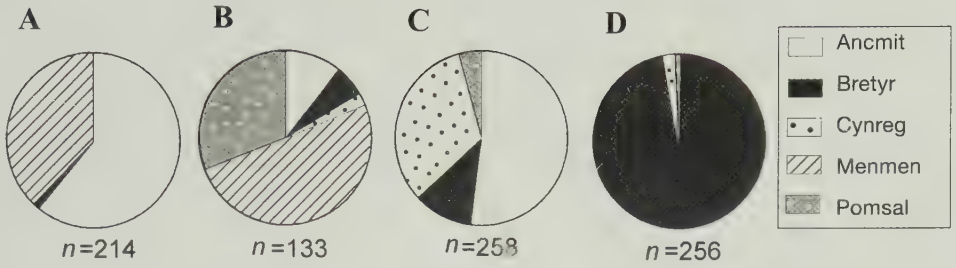

Figure 3

Most abundant forage fish (<150 mm) caught by gill nets in the Navesink River in New Jersey in 2007 and the total number of fish captured per season: (**A**) spring catch, (**B**) summer catch from station A at salinity front, (**C**) summer catch from station B at channel, and (**D**) fall catch. Forage fish species include the bay anchovy (*Anchoa mitchilli*, [Ancmit in the key]), Atlantic menhaden (*Brevoortia tyrannus*, [Bretyr]), weakfish (*Cynoscion regalis*, [Cynreg]), Atlantic silverside (*Menidia menidia*, [Menmen]), and bluefish (*Pomatomus saltatrix*, [Pomsal]).

Table 3

Species, age class, year, number of fish, length range of fish (TL), mean home range (m^2), standard deviation (SD), and reaches (1–4) of the Navesink River, New Jersey, most frequented by striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) tagged ultrasonically in 2006 and 2007.

Species and age class	Year	Number of fish	Length range (TL)	Mean home range (m^2)	SD	Reaches
Striped bass	2006	17	359–597	81.7	56.97	1, 2, 3, 4
Striped bass	2007	3	445–510	72.7	39.88	1, 3, 4
Age-0 bluefish	2006	9	194–270	101.4	76.56	3, 4
Age-0 bluefish	2007	11	222–275	101.9	68.55	3, 4
Age-1+ bluefish	2006	6	320–345	132.9	85.31	2, 3, 4
Age-1+ bluefish	2007	14	310–690	126.7	67.20	1, 2, 3, 4
Weakfish	2006	8	224–535	95.1	86.78	2, 3
Weakfish	2007	21	304–480	101.1	67.29	2, 3

Home ranges of striped bass were located in reaches 3 and 4, with a few detections in reach 1 near the river mouth, in 2006 and 2007. The home ranges of weakfish (all but 2 fish were age 1+) were centered in the channels in reaches 2 and 3, at river kilometers 5–10, in both years. For bluefish, ontogenetic differences in home ranges were observed in both years. The home ranges of age-1+ bluefish were more extensive, from reaches 2 through 4, at river kilometers 4–11. The home ranges of age-0 bluefish were centered mostly in reaches 3 and 4, at river kilometers 8–12, across the front and upriver to the Red Bank basin and Swimming River. Detections of bluefish were not as specific to channel habitats as were detections of weakfish.

Some fish shifted from a primary home range to a secondary home range during their period of residence. For example (Fig. 6), an age-1+ bluefish released on year day 122 was detected in reaches 3 to 4 at receivers located from the Red Bank basin to the Oceanic Bridge. Then, beginning on year day 142, it was detected downriver in reaches 1 and 2, at receivers from Claypit Creek to Barley Point, until it passed the last receiver and out of the river on year day 152.

The signals from some fish ceased and were detected again later in the season. Some striped bass were tagged in spring, subsequently detected in reach 1, apparently exited the river, and were detected again as they returned in fall. Some striped bass and age-1+ bluefish were detected at the farthest west receiver, disappeared, and then were detected again, apparently having made excursions into Swimming River.

Discussion

Salinity fronts, prey fields, and diets

We hypothesized that striped bass, bluefish, and weakfish would be found most often in the Navesink River in the vicinity of the main salinity transition front in the

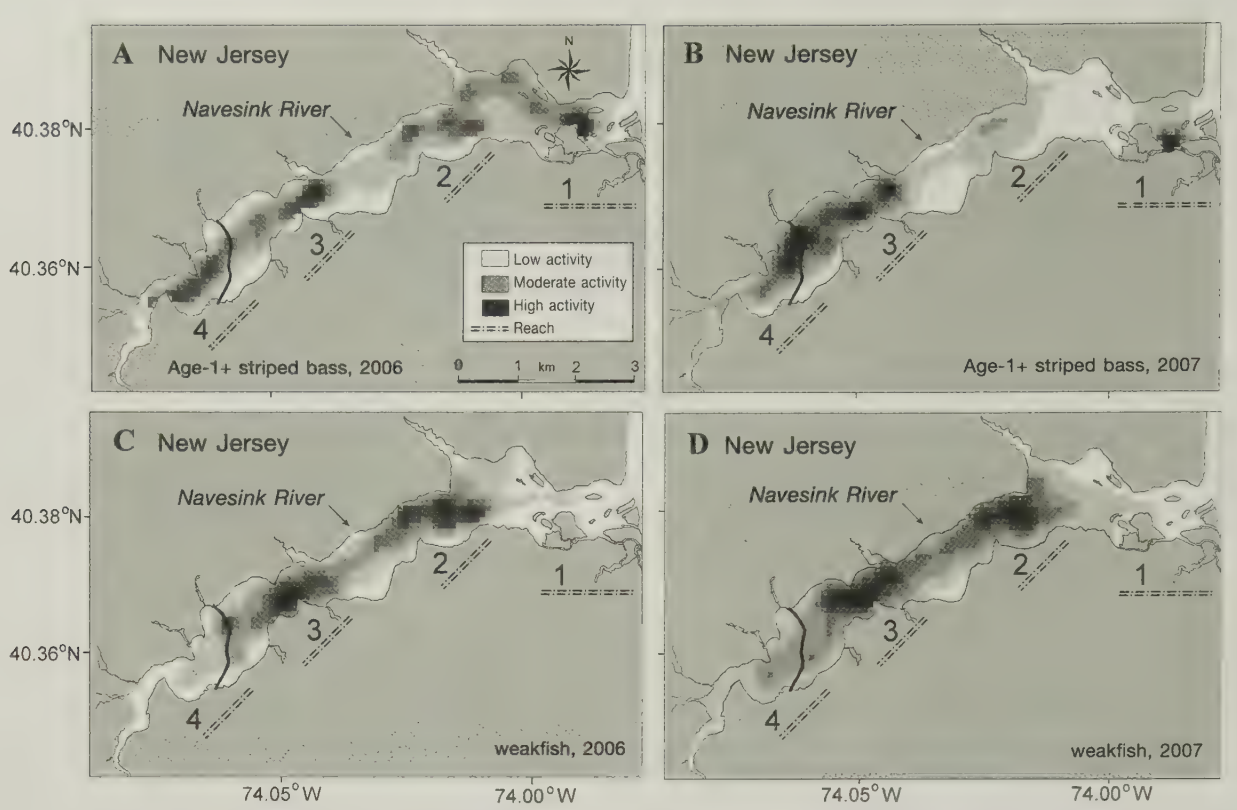

Figure 4

Plots of home ranges derived from acoustic detections of ultrasonically tagged fish in the Navesink River in New Jersey: age-1+ striped bass (*Morone saxatilis*) in (**A**) 2006 and (**B**) 2007 and weakfish (*Cynoscion regalis*) in (**C**) 2006 and (**D**) 2007. Parallel dashed lines denote reaches 1–4 of the estuary.

upper river rather than in a nearby channel. The front was well developed in summer 2007, and we were able to test the hypothesis. The data for age-0 and age-1+ bluefish conformed to the hypothesis at that time, but data for weakfish did not. Among forage fish, only Atlantic silverside was caught exclusively at the salinity front; other species were caught at both the front station and the channel station. Atlantic silverside feed on zooplankton, such as copepods, ostracods, mysids, and the young stages of many estuarine organisms (Collette and Klein-MacPhee, 2002), and zooplankton productivity is known to be concentrated at salinity fronts (Morgan et al., 1997; Martino and Houde, 2010). More Atlantic silverside were found in stomachs of fish collected at the salinity front than in stomachs of fish captured at the channel. In and around the front, chlorophyll-*a* concentration was highest as expected, and high turbidity was limited to locations upriver from the front. The abundance of Atlantic menhaden particularly is associated with patches of high chlorophyll-*a* concentration that result from phytoplankton blooms (Friedland et al., 1996; Collette and Klein-MacPhee, 2002); however, Atlantic menhaden were collected at both the front and channel stations in summer. In fall, in the absence of a defined hydrographic front, Atlantic menhaden were abundant at both stations.

The estuarine turbidity maximum does not control the availability of all prey resources that support the 3 predator species that we investigated. Atlantic menhaden and the majority of other forage fish were not limited to the area of the estuarine turbidity maximum. Invertebrate prey, particularly blue crabs and sand shrimp, were almost as important as Atlantic menhaden by percent weight in the predator diets in spring and summer. These 2 invertebrate prey species are abundant throughout the Navesink River (Meise and Stehlik, 2003; senior author, unpubl. data). We believe that, in addition to the main salinity front, other areas in the Navesink River have hydrodynamics and benthic habitats that are suitable for supporting the 3 predator species.

We found that the diets of bluefish and weakfish in 2007 generally contained the same major prey taxa. Other researchers have recognized dietary overlap with these 2 species and with striped bass (Hartman and Brandt, 1995; Wuenschel et al., 2013). The fish species that are the major prey customarily consumed by bluefish, weakfish, and striped bass in mid-Atlantic estuaries and nearshore areas are bay anchovy, Atlantic menhaden, and Atlantic silverside (Juanes and Conover, 1994; Buckel and Conover, 1997; Taylor et al., 2007).

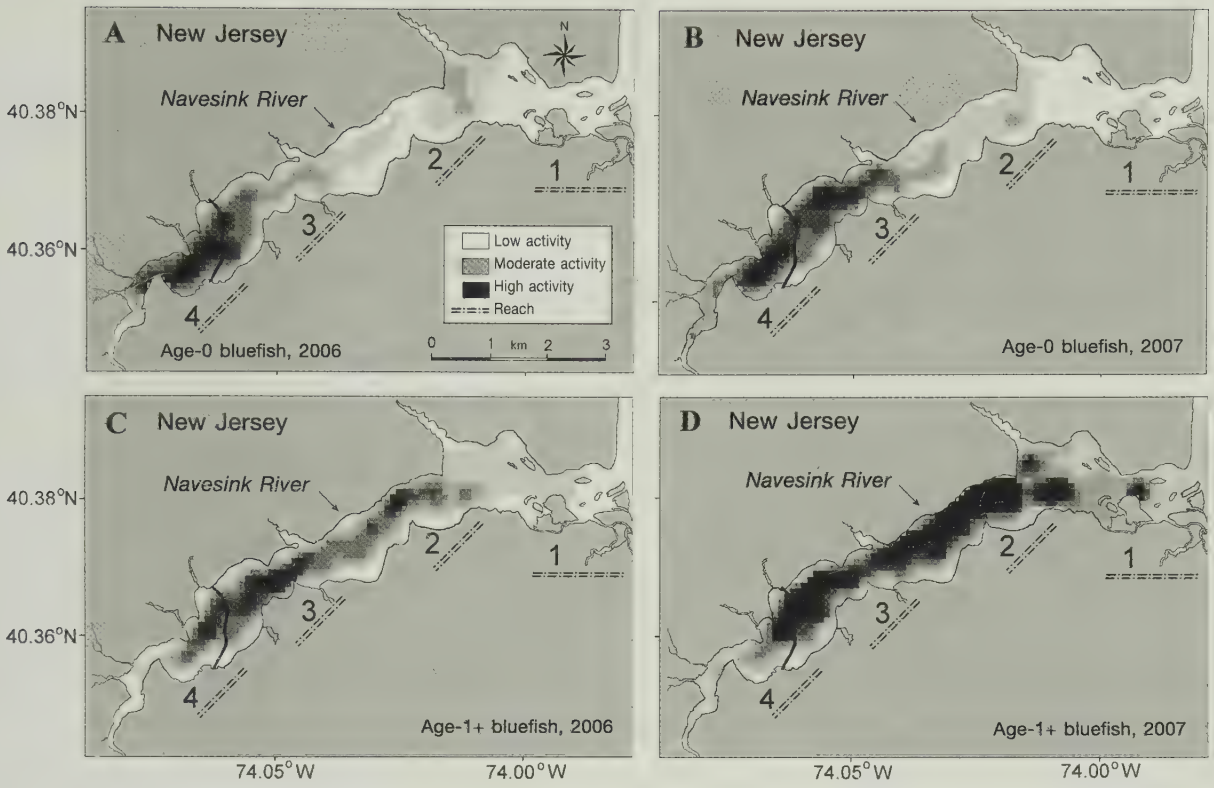

Figure 5

Plots of home ranges derived from acoustic detections of ultrasonically tagged fish in the Navesink River in New Jersey: age-0 bluefish (*Pomatomus saltatrix*) in (**A**) 2006 and (**B**) 2007 and age-1+ bluefish in (**C**) 2006 and (**D**) 2007. Parallel dashed lines denote Reaches 1–4 of the estuary.

The increased proportion of fish in the predator diets as the year progressed is attributable to 2 factors: 1) increased availability of fish prey and 2) growth of predators that allowed them to catch larger prey. The proportion of fish in relation to invertebrates in the diets of young bluefish, weakfish, and striped bass similarly has been reported to increase in other estuaries during the summer (Hartman and Brandt, 1995; Woodland et al., 2011) as forage fish grow to available size.

In mid-Atlantic estuaries, the fluctuating availability of Atlantic menhaden has had a key effect on diets of predatory fish. In the Chesapeake Bay, Atlantic menhaden dominated the diets of striped bass in the 1950s (Griffin and Margraf, 2003). They also contributed more than 60% by weight to the diet of age-2+ bluefish, striped bass, and weakfish in 1990 and 1992 (Hartman and Brandt, 1995). Although Atlantic menhaden were important in the diets of bluefish and weakfish in the Navesink River in 1998, 1999, and 2007, they were absent from the stomachs of age-0 bluefish collected in nearby Sandy Hook Bay in the 1980s (Friedland et al., 1988). The low abundance of Atlantic menhaden in the mid-Atlantic region in the 1990s and 2000s (Ferry and Mather, 2012; Pikitch et al., 2012) led to their decrease in the diets of striped bass in Chesapeake Bay and was suspected to be linked to poor physical condition of the striped bass themselves (Uphoff, 2003; Walter et al., 2003; Jacobs et al., 2009).

Home ranges and habitat associations of predators

Our study is the first to map the home ranges of 3 predators at the same location and time, to examine stomach contents, and to collect potential prey. The results of this study were consistent between 2006 and 2007, both in location and in dimension of home ranges. We found that home ranges were fairly small and similar in size among the 3 predators, indicating that the animals lock into small core areas or hotspots. The centers of home ranges were often situated in one of the deeper channels or basins directly downriver from the salinity front, particularly for weakfish. Age-0 bluefish was the only fish cohort that was detected consistently on both sides of the salinity front, in reach 4. Age-1+ bluefish had larger home ranges than age-0 bluefish, possibly because their greater body size allowed greater swimming speed (Beamish, 1978; Stehlik, 2009). Home ranges overlapped spatially, yet the occupation of those spaces was separated temporally. The overlap in the diets of predators parallels the overlap of their home ranges. The dimensions of the home ranges of these 3 predators have been found to be similar in other small

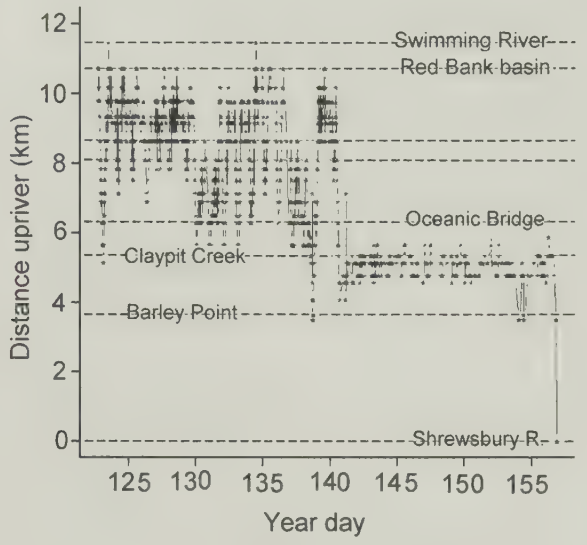

Figure 6

Acoustic detections of an age-1+ bluefish (*Pomatomus saltatrix*) that was 635 mm in total length and tracked in 2007 in the Navesink River, New Jersey. Dashed lines indicate geographical locations at the given distances from the mouth of this river.

estuaries (core areas with diameters of 0.5–1.0 km) in New Jersey (Grothues and Able, 2007; Ng et al., 2007; Able et al., 2012; Turnure et al., 2015). Striped bass in the Hudson River were tracked over many kilometers, but their movements occurred seasonally rather than daily (Wingate and Secor, 2007).

Within the home range of an individual fish, irregular diel or tide-related movements ≥1 km were noted in both 2006 and 2007 (Fig. 6). Results of general additive modeling with the 2006 telemetry data indicate that some of the variability in the daily positions was attributable to tide or time of day, but the telemetry data were complex and unclear because of extreme variability among individual fish (Manderson et al.[1]).

The results of the analysis of data from telemetric tracking augmented the results of the analysis of data from gill net sampling, showing that home ranges of the 3 predator species were not localized or limited to the area of the salinity front in the west of the Navesink River. Undoubtedly, the gill net sampling in 2007 did not provide a complete picture of the use of the Navesink River by the 3 predators because the gill nets were placed only in the upper river, separated by a distance of about 2 km. However, our study was designed on the basis of the results of the Scharf et al. (2004) study in which gill nets were used throughout the river. In that study, the greatest abundances of bluefish and weakfish in all 3 seasons occurred at their station 13 (close to the Red Bank basin, reach 4 in our study), and secondarily at station 10 (in the lower river near the mouth of Claypit Creek, reach 2 in our study) (Scharf et al., 2004; senior author, unpubl. data).

Combining hydrography, gill-net sampling, and telemetry allowed us to investigate the use of the estuarine habitat by the 3 dominant predators on a variety of temporal and spatial scales. Environmental forcing, as discussed in Manderson et al. (2014), broadly controls the residence times of fish in the Navesink River. Within the time of its estuarine residence, a fish uses a home range for a duration of days or weeks. Stomach contents are representative of the activity of about 1 d, and telemetric data shed light on hourly, daily, and seasonal activities. Hydrographic investigations detect areas where high chlorophyll-*a* concentration is favorable for zooplankton growth, and gill net sampling pinpoints concentrations of piscine prey. Tracks of individual fish show short-term diel or tide-related upriver and downriver movements of about 1 km, but further analyses of these movements would be needed to discover whether they originate from tides, light availability, prey presence, or a suite of influences. We determined that even in a small, 10-km^2 estuary, multiple reaches of the Navesink River system contain habitat of the quality needed to support the survival and growth of bluefish, weakfish, and striped bass from days to months. These advantageous habitats change in location with the seasons and are not limited to the estuarine turbidity maximum or the main salinity transition front.

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Age and growth of sheepshead (*Archosargus probatocephalus*) in Tampa Bay, Florida

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Abstract—The sheepshead (*Archosargus probatocephalus*) is common in coastal waters from the Chesapeake Bay to Texas in the United States and supports a viable recreational and commercial fishery throughout much of its range. Otoliths were extracted from 2549 sheepshead collected from 1993 through 2009 in Tampa Bay, Florida, during routine sampling by the Fisheries-Independent Monitoring program of the Florida Fish and Wildlife Conservation Commission. Sheepshead ranged in size from 107 to 524 mm fork length (FL). Age of sheepshead was estimated by counting annuli (opaque zones) in thin-sectioned sagittal otoliths. Marginal-increment analysis of sheepshead from ages 1 to 6 indicated that a single opaque ring was formed on an otolith each year between May and June. In Tampa Bay, sheephead reached a maximum age of 15 years. Males and females experienced rapid growth through age 6; growth rate decreased markedly thereafter. Although von Bertalanffy growth models were biologically similar between sexes, they were found to be statistically different (female [FL=419.1 $(1-e^{-0.272(age+1.009)})$]; males [$FL$=422.5 $(1-e^{-0.255(age+1.115)})$]). Tampa Bay sheepshead are typically smaller at a given age than those in more northern climates and not as long lived. Differences in regional growth models may be attributed to differences in mortality, ontogenetic shifts in habitat, genetic variation, or sampling design.

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The sheepshead (*Archosargus probatocephalus*) occurs from Nova Scotia (Gilhen et al., 1976) to Brazil (Caldwell, 1965) and is common in coastal waters from Chesapeake Bay to Texas in the United States (Bigelow and Schroeder, 1953; Collette and Klein-MacPhee, 2002). Two subspecies of sheepshead have been reported within its U.S. range: *A. p. probatocephalus*, found along the Atlantic coast and into the Gulf of Mexico as far north as Steinhatchee, Florida, and *A. p. oviceps*, which occurs in the Gulf of Mexico from St. Marks River, Florida, to Campeche Bank, Mexico (Caldwell, 1965). Subspecific distinction is based partly on pigmentation (size and number of vertical body bars) and meristic counts (lateral line scales, gill rakers, and dorsal fin spines and rays), both of which overlap considerably between the 2 subspecies (Caldwell, 1965). Results of recent genetic analyses in which mtDNA of sheepshead from the Gulf of Mexico and South Atlantic indicated that a single panmictic population of sheepshead exists within the range of this species from Texas through North Carolina (Anderson et al., 2008; Seyoum et al., in press). More detailed microsatellite analysis, however, has revealed a significant genetic break at the subspecies boundary in the Florida panhandle (Apalachee Bay), providing genetic support for the validity of 2 subspecies of sheepshead within its range in the United States (Seyoum et al., in press).

The combined recreational and commercial landings of sheepshead from the gulf coast of Florida between 1990 and 2009 made up 19–44% of the total annual landings of sheepshead for all U.S. states in the Gulf of Mexico (National Marine Fisheries Service, Fisheries Statistics and Economics Division commercial annual landings statistics, available from website, accessed June 2014, and Marine Recreational Information Program time-series data, available from website). The combined annual landings from the gulf coast of Florida peaked at 1755.6 metric tons in 1992; from 1996 to 2009, they averaged less than half that amount (841.3 metric tons/year) because of enactment in 1995 of a Florida constitutional amendment that limits

the use of entangling nets and mandates the institution of minimum size and bag limits for recreational fishermen (Munyandorero et al.[1]). Historically, more sheepshead have been landed by recreational fishermen than commercial fishermen (70–95% of the combined annual landings during 1990–2009) along Florida's gulf coast (Munyandorero et al.[1]).

Growth has been described for larval and early juvenile sheepshead from Florida waters (Parsons and Peters, 1989). Elsewhere, age and growth studies of juvenile and adult sheepshead have been conducted in Georgia (Music and Pafford[2]), North Carolina (Schwartz, 1990), South Carolina (Wenner[3]), Louisiana (Beckman et al., 1991), and northwest Florida (Dutka-Gianelli and Murie, 2001). Validated (Music and Pafford[2]) and unvalidated (Schwartz, 1990) ages have been determined also from scales. However, Dutka-Gianelli and Murie (2001) reported that scales of sheepshead older than 3 years resulted in underestimated ages, and scales from sheepshead aged 2 or more years have been described as unreadable (Schwartz, 1990; Wenner[3]).

Validated ages determined from otolith sections have been used to estimate von Bertalanffy growth parameters for sheepshead from Louisiana (Beckman et al., 1991), South Carolina (Wenner[3]), and northwest Florida (Dutka-Gianelli and Murie, 2001). All 3 studies noted a high variability in size at age for sheepshead, reported von Bertalanffy growth parameters, and the predicted sizes at age varied considerably among the 3 studies (Dutka-Gianelli and Murie, 2001). Each study relied almost exclusively on the fishery (commercial or recreational) for its samples. Beckman et al. (1991) indicated that because the gear types used were more apt to catch certain sizes of fish than others and because fishermen occasionally sorted the catch before supplying the researchers with samples, the age and size structures of the sheepshead analyzed probably did not represent the overall population of sheepshead in Louisiana. Other researchers also have determined that reliance upon samples obtained only from the fishery can cause misrepresentation of the size distribution and age structure of a population (Miranda et al., 1987; Hilborn and Walters, 1992; Wilson et al., 2015).

By design, we used multiple gear types and fisheries-independent methods to provide a more representative sample across size and age classes of sheepshead, therefore generating estimates of growth parameters more representative of the true population. Otolith annuli (opaque zones) were validated to determine age and growth parameters for sheepshead, and these estimates were then compared with those previously reported for sheepshead from other geographical regions.

Materials and methods

Sheepshead were collected in Tampa Bay, Florida (Fig. 1), a large estuary on the west coast of Florida that has an average depth of approximately 3 m and a maximum depth of 13 m (Comp and Seaman, 1985). All sheepshead were captured from 1993 through 2009 by the Fish and Wildlife Research Institute's Fisheries-Independent Monitoring program during routine sampling with haul seines, trawls, gill nets, and trammel nets (Table 1). Haul seine and trawl samples were collected at both stratified-random and fixed sites; gill net collections were made at stratified-random sites. More detailed information about the sampling gears and protocols used by the Fisheries-Independent Monitoring program can be found in Tremain and Adams (1995), Nelson et al. (1997), Nelson (1998), and Winner et al. (2010). Sheepshead were also taken as bycatch from trammel nets, which had been set on visually detected schools of striped mullet (*Mugil cephalus*), red drum (*Sciaenops ocellatus*), or common snook (*Centropomus undecimalis*). For each fish, we recorded standard length (SL), fork length (FL), and total length (TL) to the nearest millimeter; sex; and total weight to the nearest 0.1 g before extraction of sagittal otoliths, which were then rinsed, cleaned, and stored dry for further examination.

Sex ratios of sheepshead were compared with a hypothetical 1:1 sex ratio by using the *G*-test (Sokal and Rohlf, 1981). Length distributions also were compared between sexes by using the Kolmogorov–Smirnov (KS) 2-sample test (Proc Nparlway procedure in SAS[4] software, vers. 5.1 (SAS Institute Inc., Cary, NC). Linear regression for all sheepshead collected was used to calculate sex-specific length–length and length–weight relationships (Proc Reg procedure in SAS software) for untransformed and transformed ($\log_{10}$) data, respectively, and these relationships were compared through analysis of covariance (ANCOVA; Snedecor and Cochran, 1967). Data from all fish collected were pooled when slopes and intercepts for sex-specific regressions were not significantly different. All significance testing was conducted at $P \leq 0.05$.

Three or four thin (~0.5 mm) transverse sections were cut at or adjacent to the core of the left sagitta with a Buhler Isomet low-speed saw equipped with a diamond blade; a right sagitta was sectioned when the left sagitta was missing or had been damaged. Oto-

[1] Munyandorero, J., J. O'Hop, and C. Guenther. 2011. An assessment of the status of sheepshead in Florida waters through 2009. Florida Fish Wildl. Conserv. Comm., Fish Wildl. Res. Inst., IHR 2011-003, 137 p. Fish and Wildlife Research Institute, St. Petersburg, FL. [Available from website.]

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[3] Wenner, C. 1996. Age and growth of sheepshead, *Archosargus probatocephalus*, from South Carolina waters with some preliminary management concepts, 17 p. S. Carolina Dep. Nat. Resour., Charleston, SC.

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

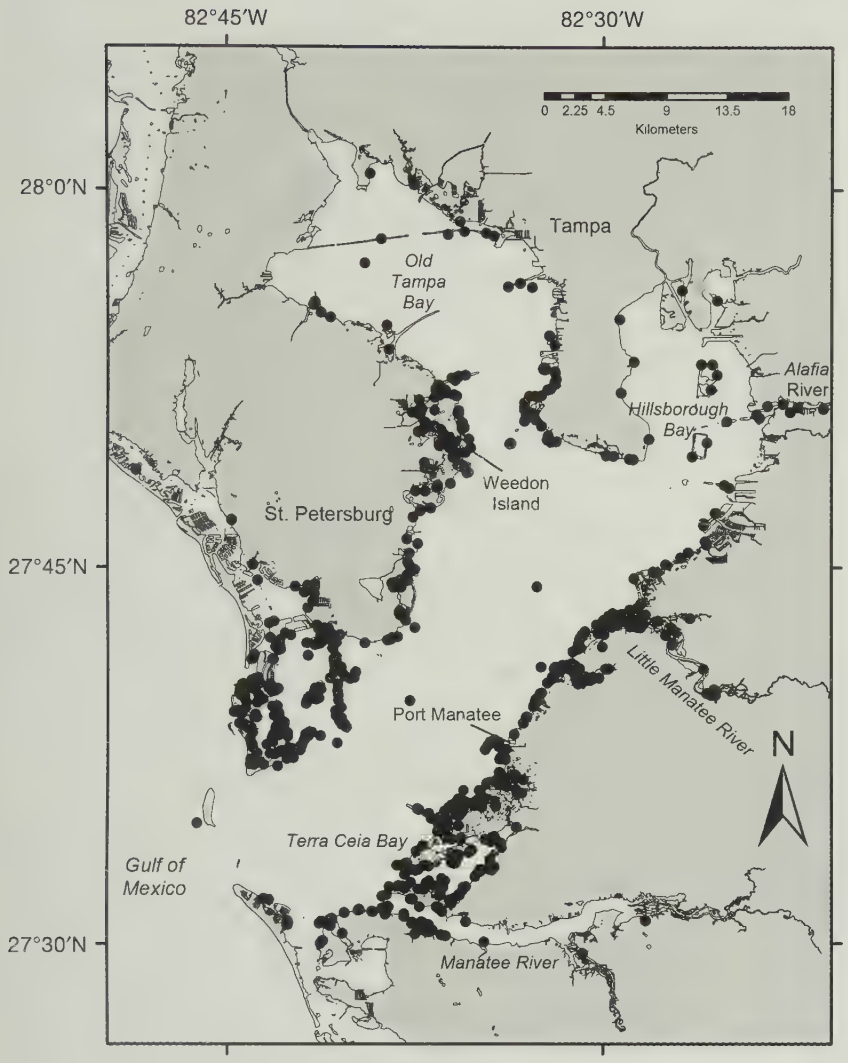

Figure 1

Sampling locations (indicated by black circles) in Tampa Bay, Florida, where sheepshead (*Archosargus probatocephalus*) were collected during 1993–2009 for age and growth analysis under the guidance of the Fisheries-Independent Monitoring program of the Florida Fish and Wildlife Conservation Commission.

lith sections were mounted on microscope slides by using Histomount solution (Thermo Fisher Scientific, Waltham, MA). With a dissecting microscope (8–25× magnification), 2 or 3 readers independently counted the opaque rings on each otolith twice under reflected light. Readers counted rings without knowing the sex, length, or capture date of specimens. Disagreements in annulus counts were resolved by at least 2 readers, without knowledge of previous counts. If an annulus count could not be agreed upon after reexamination, the otolith was rejected from the age and growth analysis.

Validation of annuli counts was completed through marginal-increment analysis, which provided indirect evidence at the otolith margin of the periodicity of annulus formation. Measurements from the core to the proximal edge of each annulus, along the ventral sulcal ridge, were completed with a digital image-processing system for all otoliths processed from 1995 through 1998. The marginal increment was calculated as a percentage by dividing the distance from the terminal annulus to the marginal edge by the distance between the last 2 annuli formed on the otolith and multiplying by 100. Monthly marginal-increment statistics (25th, 50th, and 75th percentiles) with all age classes pooled were calculated for February 1995–December 1998, the period during which monthly samples were collected consistently. Additionally, monthly marginal-increment statistics were plotted, with months pooled across all years (1995–1998), for individual age classes (ages 1–6 only). Fish age 7 and older were excluded from these age-class–specific analyses because of low sample size across sampled months.

Age of each sheepshead was calculated on the basis of annulus count, marginal increment, date of capture, and an assumed hatching date of 1 April (an assumption based on spawning and larval recruitment; Parsons and Peters, 1989; Tucker and Alshuth, 1997). Therefore, sheepshead collected in February and March that had recently formed an annulus, as determined by a low (<30%) marginal increment were assigned an age of one less than the ring count. Fish collected in April, May, or June that were about to deposit an annulus (at >80% marginal increment) were assigned an age of one more than the ring count. All other fish were assigned an age equal to the ring count. Daily age was calculated on the basis of the age and the number of days that had passed between 1 April and the date of collection:

$$(\textit{integer age} + \textit{number of days})/365. \quad (1)$$

The *G*-test was used to compare sex ratios for all fish collected and subsets of fish kept for or eliminated from the aging analysis. Lengths of retained and eliminated sheepshead were compared by using the KS 2-sample test (Proc Nparlway procedure; SAS, 2006). The KS test was also used to compare age-frequency distributions between the sexes.

The von Bertalanffy (1957) growth equation,

$$L_t = L_\infty(1-e^{-k(t-t_0)}), \quad (2)$$

Table 1

Descriptive statistics for fork length and age (mean, minimum, maximum, and standard deviation [SD]) and total catch of sheepshead (*Archosargus probatocephalus*) collected in Tampa Bay, Florida, in 1993–2009, by gear type.

		Fork length (mm)				Age (years)			
Gear type	Number of fish	Mean	Min	Max	SD	Mean	Min	Max	SD
Small haul seines	52	287.0	153	415	65.2	3.5	0.9	6.9	1.6
Large haul seines	1931	299.4	107	524	63.7	4.1	0.5	15.2	2.1
Purse seines	50	256.1	173	465	62.3	3.1	1.2	7.9	1.6
Gill nets	62	284.2	158	409	59.3	3.7	1.0	9.6	2.0
Otter trawls	36	254.6	159	383	55.7	3.4	1.3	11.6	2.3
Trammel nets	367	322.9	146	458	48.3	4.5	0.6	11.5	1.8
Unknown	51	318.2	190	433	52.8	4.8	1.3	10.5	1.7
Total catch	2549								

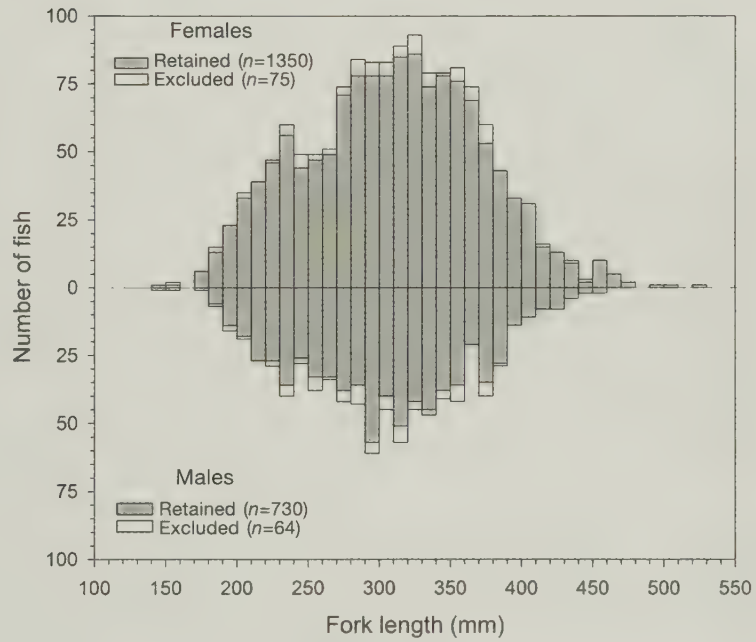

Figure 2

Length-frequency distributions for female and male sheepshead (*Archosargus probatocephalus*) collected in Tampa Bay, Florida, 1993–2009. Sheepshead that were retained and excluded (otolith identified as unreadable) from the age and growth analysis are depicted. Sheepshead for which there was both age and sex information but which did not have a measured fork length were excluded from this plot

where L_t = the observed FL at time t;
L_∞ = the asymptotic FL;
k = the growth coefficient;
t = the observed age; and
t_0 = the hypothetical age at size zero, was fit by nonlinear regression (Proc NLin procedure, Marquardt routine in SAS software) for sex-specific observed age and length data.

Growth models for males and females were compared with an approximate randomization test (Helser, 1996).

Results

Size and sex composition

Sheepshead (n=2549) ranging in size from 107 to 524 mm FL were collected in Tampa Bay (Fig. 1) with a variety of gear types (Table 1). Although sampling was done throughout the estuary, most specimens were collected along the shoreline in the middle to lower portions of the estuary with a large haul seine (n=1931, 75.8%) or a trammel net (n=367, 14.4%). Together, the other gear types caught less than 10% of the specimens used in this study.

Sex was determined for 93% of the sheepshead collected. The majority of the specimens for which sex was not determined were immature (≤2 years old) fish for which gonad samples were too small to allow sex determination. The sex ratio of males to females (1:1.75) in our samples was significantly different from 1:1 (G-test: 177.69, df=1, P≤0.001). Mean length of females (308.5 mm FL) was slightly greater than that of males (302.0 mm FL), but length-frequency distributions did not differ significantly between sexes (Fig. 2; KS test: 0.058, P≥0.05). Neither the slopes nor the intercepts differed significantly in the sex-specific length–length regressions (ANCOVA: P>0.05); therefore, all sheepshead data were pooled to elucidate relationships among SL, FL, and TL (Table 2). All length–length regressions exhibited high coefficients of determination (r^2≥0.988) (Table 2). Sex-specific length–

Table 2

Length–length and length–weight regressions for sheepshead (*Archosargus probatocephalus*) collected in Tampa Bay, Florida, 1993–2009. Measurements include standard length (SL) in millimeters, fork length (FL) in millimeters, total length (TL) in millimeters, and total weight (WT) in grams. Values in parentheses are standard errors. Sex-specific length–weight regressions were necessary because male and female regressions had significantly different intercepts. r^2=coefficient of determination.

			$Y = a + bX$		
Y	X	n	a	b	r^2
TL	FL	2218	0.853 (0.491)	1.094 (0.002)	0.995
TL	SL	2344	12.676 (0.742)	1.215 (0.003)	0.988
FL	TL	2218	0.621 (0.448)	0.910 (0.001)	0.995
FL	SL	2218	11.318 (0.629)	1.109 (0.002)	0.990
SL	FL	2218	−7.559 (0.582)	0.893 (0.002)	0.990
SL	TL	2344	−7.178 (0.627)	0.813 (0.002)	0.988
Log_{10}(WT), females	Log_{10} (FL)	1406	−4.508 (0.031)	2.960 (0.013)	0.976
Log_{10}(WT), males	Log_{10} (FL)	792	−4.367 (0.038)	2.899 (0.015)	0.978

weight regressions were necessary because regressions for males and females had significantly different intercepts (ANCOVA: F=32.15; df=1, 2196; $P \leq 0.001$), but r^2 was high for both males (≥0.978) and females (≥0.976) (Table 2).

Age determination and validation

Marginal-increment analysis of otoliths from sheepshead, with all age classes pooled, indicated that a single opaque ring formed annually between May and June (Fig. 3). Median marginal increment reached a consistent minimum from late spring to early summer (May 1995, June 1996, June 1997, June 1998) and a consistent maximum during winter (February 1995, January 1996, February 1997, January 1998). Large interquartile ranges in the months before and during opaque-ring deposition indicated that many individuals had either just deposited (and therefore had a low increment width) or were about to deposit an opaque ring (and had a high increment width). Pooling monthly marginal increments across all years for individual age classes (ages 1–6) also indicated that for each age class a single opaque ring was deposited during the late spring or summer (Fig. 4).

Otoliths of 2549 sheepshead were examined for age; 154 (6.0%) were excluded from the aging analysis (because there was no agreement among readers or because an otolith was damaged), and 169 (6.6%) were excluded from sex-specific age analyses (because no sex data were available). The male to female sex ratio for the sheepshead retained in the aging analysis (1:1.79) did not differ significantly from that of the overall sample (1:1.75; G-test: 0.340, df=1, P>0.05). But the male-to-female sex ratio for sheepshead excluded from the aging analysis (1:1.20) was significantly different from that of sheepshead retained in the aging analyses (G-test: 5.06, df=1, P<0.05). Sex-specific length-frequency distributions of fish excluded from the analysis did not differ significantly from those retained (Fig. 2; KS test: females, 0.084, P>0.05; males, 0.102, P>0.05).

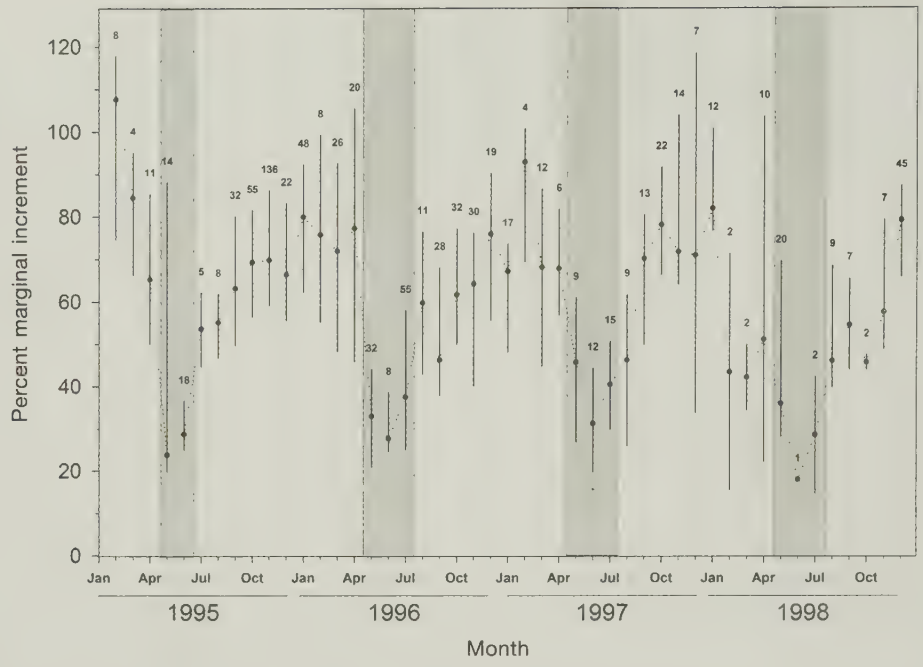

Figure 3

Median monthly percent marginal increment (indicated by black points) for otoliths of sheepshead (*Archosargus probatocephalus*), all ages combined, collected in Tampa Bay, Florida, 1995–1998. Vertical lines indicate the interquartile ranges. Numbers above monthly percent marginal increments indicate sample sizes. Months of minimal marginal increment (indicating annuli deposition) are highlighted in gray boxes.

Age and growth

Sheepshead ranged from <1 year to 15 years of age, and the mean ages of males (3.67 years) and females (3.73 years) were similar (Fig. 5). The overall age-frequency distributions of males and females (Fig. 5) did not differ significantly (KS test: 0.032, $P>0.05$). Sheepshead of ages 2–4 accounted for more than half of the individuals collected (62.9%), but sheepshead aged 7 or older were relatively rare (7.9%). The oldest fish (sex not determined: 524 mm FL, 14.7 years; male: 404 mm FL, 14.9 years; and female: 345 mm FL; 15.2 years) were collected in a large haul seine.

Observed length at age was variable for both sexes (Fig. 6). Growth was relatively rapid for both males and females. By age 1, sheepshead, regardless of sex, reached a size predicted to be more than 40% of L_∞, and, by age 6, they had reached sizes greater than 80% of L_∞. Growth rates of both sexes slowed after age 6. Males achieved a slightly greater L_∞ than females (3.4 mm FL greater), but females grew at a slightly higher rate (as measured by K; Table 3, Fig. 6) than males. The von Bertalanffy growth models for males and females (approximate randomization test: $P<0.01$) were significantly different. Although predicted size at age was greater for females than for males in all age classes from ages 1 through 10 (Table 4), the difference between predicted size at age between sexes was minimal, 7 mm FL or less (mean difference of 3.3 mm FL) across all age classes.

Discussion

Age determination and validation

Sheepshead age and growth has been studied by using both scales and sagittal otoliths. Although scales have been used to age sheepshead (Music and Pafford[2]; Schwartz, 1990; and Wenner[3]), validation of annuli on scales of sheepshead has indicated that scales are not as reliable as otoliths for aging this species. Music and Pafford[2] could validate scale annuli only in sheepshead younger than age 5, and annuli in scales of sheepshead older than age 2 have been reported to be unreadable (Schwartz, 1990; Wenner[3]). Age has been underestimated in sheepshead and other fish species when scales were used, and age estimates from the use of scales have been lower than those derived from otolith sections (Beamish and McFarlane, 1983; Carlander, 1987; Lowerre-Barbieri et al., 1994; Dutka-Gianelli, 1999). In our discussion, the only studies considered in growth comparisons are those in which ages were estimated on the basis of validated otolith annuli.

We used marginal-increment analysis, which has been used to validate annulus deposition in the sag-

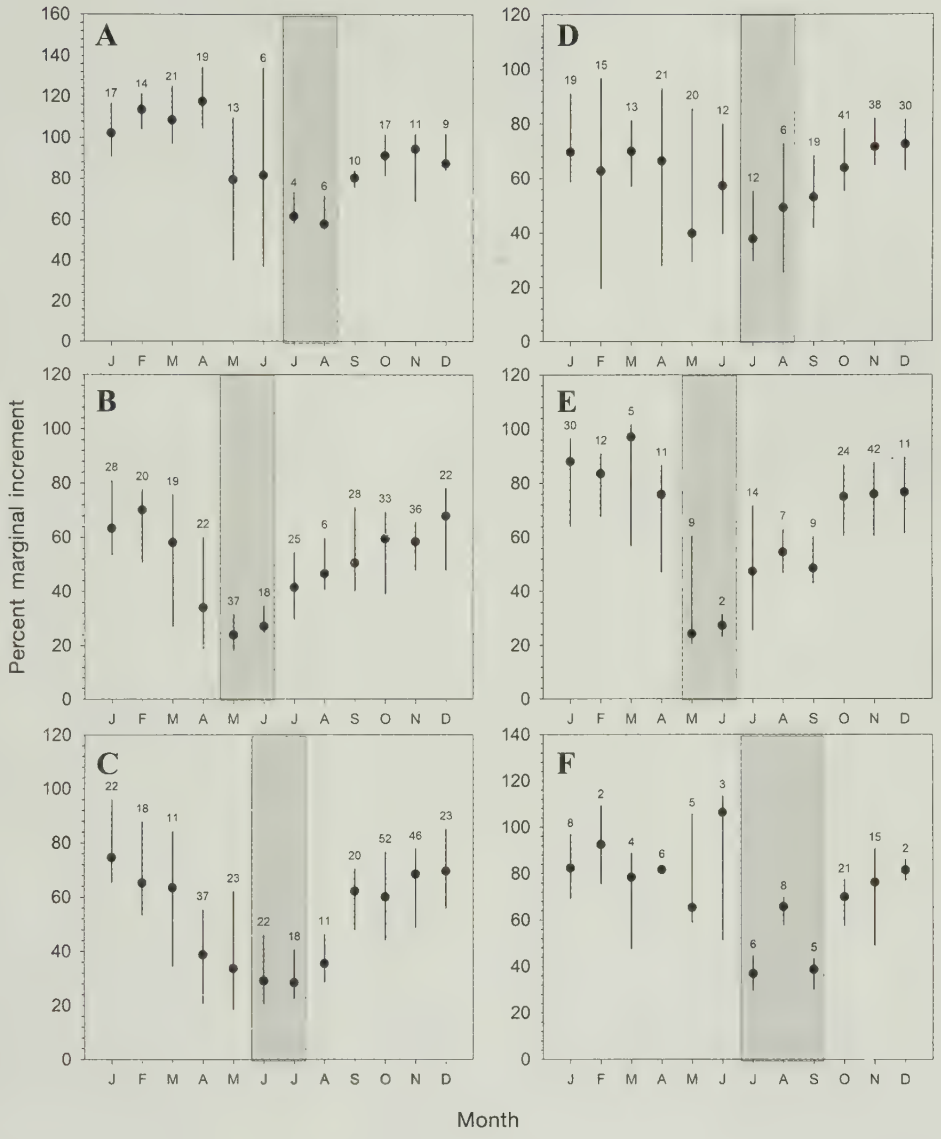

Figure 4

Median monthly percent marginal increment (indicated by black points) for otoliths of sheepshead (*Archosargus probatocephalus*) collected in Tampa Bay, Florida, 1995–1998, by individual age classes: (**A–F**) ages 1–6. Vertical lines represent the interquartile ranges, and numbers above percent marginal increments represent the sample sizes. Months of minimal marginal increment (indicating annuli deposition) are highlighted in gray boxes.

ittae of sheepshead from other areas. Studies from Louisiana (Beckman et al., 1991), northwest Florida (Dutka-Gianelli and Murie, 2001), and South Carolina (individual age classes, <age 5; Wenner[3]) used marginal-increment analysis to validate the deposition of a single annulus per year. Chemical marking with oxytetracycline validated the annual deposition of a single opaque ring in sheepshead of ages 2–3 (Dutka-Gianelli and Murie, 2001). Each of these studies reported that a single annulus was deposited from late winter to spring (March–May for sagittae)—a finding similar to that of our study (May–June).

In our study, fish older than age 7 were uncommon; therefore, we could not analyze marginal increments for those fish by age class to validate annulus deposition. Examination of fish aged 7–14, as a group, showed that annuli formed at the same time as fish in younger age classes. Although we presume that these older fish laid down a single opaque ring each year, ages of fish older than age 6 may sometimes have been misinterpreted (Beamish and McFarlane, 1983). It would be valuable in future studies in the Tampa Bay area that more age data be collected from larger and older sheepshead to further elucidate annulus deposition in these older fish.

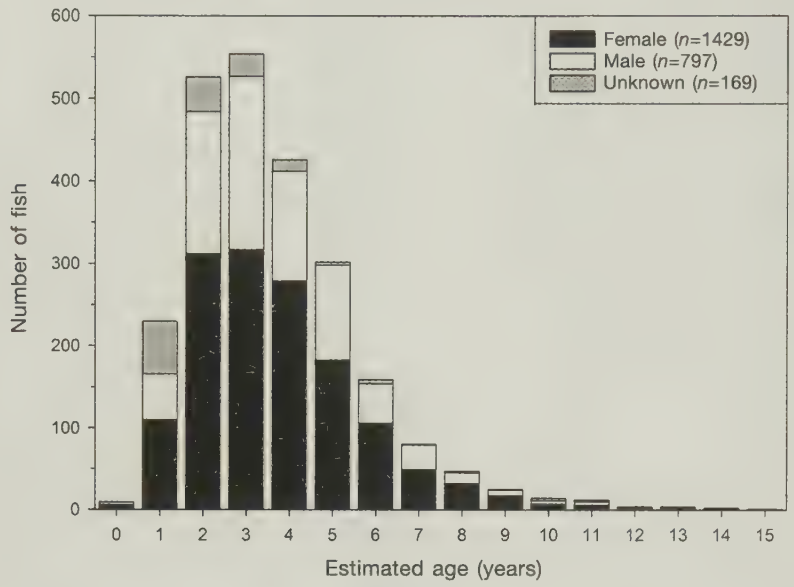

Figure 5

Age-frequency distributions for sheepshead (*Archosargus probatocephalus*) collected in Tampa Bay, Florida, 1993–2009.

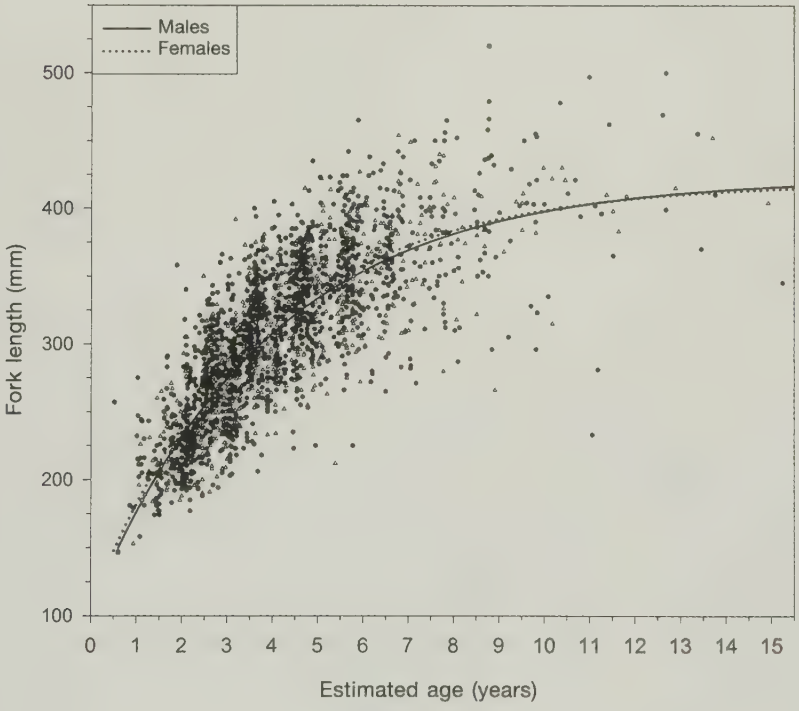

Figure 6

Observed fork lengths and estimated ages of female (indicated by black circles) and male (indicated by open triangles) sheepshead (*Archosargus probatocephalus*) collected in Tampa Bay, Florida, 1993–2009. The lines depict the predicted size at age from the von Bertalanffy growth models for males and females. Von Bertalanffy growth parameters for both sexes are presented in Table 3.

Growth

Results of growth studies of sheepshead have shown marked geographic variation. Sheepshead in northern areas of the Gulf of Mexico and Atlantic are longer lived and grow larger than those in Florida (Beckman et al., 1991; Wenner[3]; Dutka-Gianelli and Murie, 2001). We found that the growth of sheepshead in Tampa Bay was similar to that reported farther north along the gulf coast of Florida. Sheepshead from Tampa Bay were observed to reach at least 524 mm FL and to reach an estimated maximum age of 15 years. Dutka-Gianelli and Murie (2001) collected sheepshead in northwest Florida with a similar maximum age (15 years) and size (522 mm FL). In contrast, sheepshead from Louisiana (Beckman et al., 1991) lived longer (20 years) and grew larger (563 mm FL) than sheepshead collected in Florida (Dutka-Gianelli and Murie, 2001; our study). Specimens collected in South Carolina (Wenner[3]) included the greatest reported estimated age for sheepshead (26 years). Wenner[3] also reported a sheepshead maximum size (560 mm FL) similar to that reported for sheepshead from Louisiana.

Fish length is a poor measure for estimating age in sheepshead. Sheepshead of similar age can differ considerably in length (Schwartz, 1990; Beckman et al., 1991; Wenner[3]; Dutka-Gianelli and Murie, 2001; our study). For example, in our study, age-5 sheephead ranged from 212 to 465 mm FL, and 350-mm-FL specimens ranged from age 2 to age 8. Length has also been seen as unreliable for estimating the age for other sparids, including red porgy (*Pagrus pagrus*; Hood and Johnson, 2000), black bream (*Acanthopagrus butcheri*; Sarre and Potter, 2000), pinfish (*Lagodon rhomboides*; Nelson, 2002), and littlehead porgy (*Calamus proridens*; Tyler-Jedlund and Torres, 2015).

Although growth models for male and female sheepshead from Tampa Bay differed statistically, the actual growth parameters were biologically very similar for the sexes. Sex-specific growth models had a significantly

Table 3

Estimates of the von Bertalanffy growth parameters, by sex, and with sexes combined: asymptotic length (L_∞), growth coefficient (k), and hypothetical age at size zero (t_0) for sheepshead (*Archosargus probatocephalus*) collected in Tampa Bay, Florida, 1993–2009. Sample sizes (n) and asymptotic standard errors (in parentheses) are listed. Combined includes female and male sheepshead, as well as sheepshead for which sex was not determined (n=169).

	Females	Males	Combined
L_∞ (mm)	419.1 (7.206)	422.5 (9.948)	418.7 (5.309)
K	0.272 (0.019)	0.255 (0.023)	0.273 (0.014)
t_0	−1.099 (0.162)	−1.115 (0.205)	−0.981 (0.107)
n	1429	797	2395

better fit for sheepshead from Louisiana waters than a model in which sexes were combined. Predicted sizes at age for Louisiana sheepshead were similar for both sexes through age 6, with a mean difference in size at age of 11.6 mm FL between the sexes (Table 4), but this difference in size was greater at older ages (25.8 mm difference in FL for ages 7–20). Despite finding no significant difference in sex-specific growth for sheepshead from northwest Florida, both sex-specific and combined-sex growth models were presented by Dutka-Gianelli and Murie (2001); mean differences in predicted size at age between sexes (11.2 mm FL) were larger than the differences we found (mean differences of only 3.3 mm FL; Table 4). Therefore, evidence of growth differences between males and females has often been varied among previous studies. For recent stock assessments of sheepshead in Florida, growth was assumed to be similar for males and females, but coast-specific growth parameters were used because growth varied significantly between the two regions (Munyandorero et al.[1]).

Our estimates of L_∞ and the t_0 (Table 3) were within 2 standard errors of those estimated for fish from Louisiana waters (males: L_∞=419, t_0= −0.901; females: L_∞=447, t_0= −1.025; Beckman et al., 1991; Table 4). Estimated L_∞ for sheepshead from South Carolina (505.0 mm FL) and northwest Florida (490.4 mm FL) were greater than those for sheepshead from either Tampa Bay or Louisiana. For sheepshead from South Carolina and northwest Florida and in our study, values of k were similar but smaller than those reported for sheepshead in Louisiana, indicating that Louisiana sheepshead reach L_∞ more rapidly. Beckman et al. (1991) found predicted lengths for age-3 Louisiana male and female sheepshead were 80% and 77% of their L_∞, respectively. We found that sheepshead in Tampa Bay are not predicted to reach 80% of L_∞ until age 5 for females (81%) and age 6 for males (83.8%). Similarly, in studies conducted in South Carolina (Wenner[3]) and northwest Florida (Dutka-Gianelli and Murie, 2001), sheepshead were predicted to reach 80% of L_∞ by age 5 and age 6, respectively. The differences in growth parameters between these latter 2 studies may be attributed to differences in sampling methods, ontogenetic habitat shifts, or estuarine-specific differences in growth or mortality. Furthermore, the variation in growth parameters between these studies may also be affected by variability in genetic composition (subspecies) among the regions where these studies were conducted.

Reliance on fishery-dependent samples can introduce size- and age-related biases that can result in misleading interpretations of fish growth and size distribution, and age structure of a population (Langler, 1978; Miranda et al., 1987; Hilborn and Walters, 1992). All the sheepshead analyzed in a Louisiana study were collected from commercial and recreational catches. Almost 60% of their fish came from catches with gill nets, which tend to be size selective, often resulting in a narrow size range of collected fish (Pope et al., 1975). Beckman et al. (1991) indicated that their sample of sheepshead was probably not representative of the Louisiana population because of gear selectivity and sorting of catches before sampling. In a South Carolina study, most sheepshead larger than 300 mm FL were caught in recreational fishing tournaments and probably represented a greater percentage of larger fish than that of the overall population (Wenner[3]). Consequently, the sampling methods of these studies could have introduced sufficient size-at-age bias to the effect that the sampled fish did not represent the population as a whole. Our fisheries-independent sampling design increased the likelihood that our data would approximately represent the size and age structure of the population of sheepshead in Tampa Bay. Specimens were collected by using a variety of gear types (a majority of specimens with the nonselective large haul seine [77%]), and at randomly selected sites (68%) that represented a variety of habitats.

Adult sheepshead have been reported to occur over hard structure (reefs, jetties, and piers) in both estuarine (Johnson, 1978; Ogburn, 1984) and offshore (Sedberry and van Dolah, 1984) waters. Sheepshead also have been reported to undergo an ontogenetic shift in habitat as juveniles (Hildebrand and Cable, 1938; Johnson, 1978), moving from shallow nursery habitats, which often include sea grasses, to hard-structure habitats of adults. Sheepshead in our study were collected from relatively shallow waters (mean depth: 1.2 m [standard error 0.02]) in the Tampa Bay estuary, whereas portions of sheepshead in the Louisiana and northwest Florida studies came from deeper, offshore areas. Render and Wilson (1992) found no significant differences in size or age between the sheepshead collected in offshore and inshore waters of Louisiana, but sample size and gear selectivity (i.e., similar among

Table 4

Estimates of the von Bertalanffy growth parameters, the asymptotic length (L_∞), growth coefficient (k), and hypothetical age at size zero (t_0), and the predicted size at age, presented in fork length (FL) in millimeters, for sheepshead (*Archosargus probatocephalus*) collected from in Tampa Bay, Florida, 1993–2009 (this study); Louisiana, 1987–1988 (Beckman et al., 1991); northwest Florida, 1997–1998 (Dutka-Gianelli and Murie, 2001); and South Carolina, 1995–1996 (Wenner[3]).

	Tampa Bay		Louisiana		Northwest Florida			South Carolina[1,2]
Growth parameters	Females	Males	Females	Males	Combined	Females	Males	Combined
L_∞ (mm FL)	419.1	422.5	447.0	419.0	490.4	475.7	509.2	505.0
k	0.272	0.255	0.367	0.417	0.260	0.280	0.230	0.290
t_0	−1.099	−1.115	−1.025	−0.901	−0.420	-0.460	-0.520	−1.109
Predicted size at ages (mm FL)								
0	109	105						139
1	183	177			151	160	150	231
2	239	232	300	294	229	237	224	299
3	282	275	345	337	289	295	283	351
4	315	308	376	365	335	339	329	389
5	340	334	398	383	371	373	366	418
6	359	354	413	395	398	398	396	440
7	373	370	423	403	419	417	419	456
8	384	382	431	409	435	431	437	469
9	393	391	436	412	448	442	452	478
10	399	398	439	415	458	450	464	485
11	404	404	442	416	465	456	473	490
12	408	408	443	417	471	461	481	494
13	411	411	444	418	475		486	497
14	413	414	445	418	479		491	499
15	414	416	446	418	482		495	500
16			446	419				502
17			446	419				503
18			447	419				503
19			447	419				504
20			447	419				504
21								504
22								505
23								505
24								505
25								505
26								505

[1] For the growth parameters, L_∞ originally presented as total length (TL; 559 mm); converted to FL, for comparison, by using TL–FL relationship given by Wenner[3].

[2] For predicted sizes at age calculated as TL (L_∞=559 mm) and converted to FL, for comparison, by using TL–FL relationship given by Wenner[3].

areas) may have obscured differences. If sheepshead undergo a habitat shift from shallow nearshore waters into deeper waters, the growth parameters we describe might not indicate the age and growth of sheepshead in the deeper habitats.

Regional differences in sheepshead growth parameters may be attributed partly to population genetics. Within the U.S. range of this species, 2 subspecies of sheepshead have been reported (Caldwell, 1965). We analyzed *A. p. probatocephalus*, which occurs along the Atlantic coast and into the Gulf of Mexico to Steinhatchee, Florida. A Louisiana study (Beckman et al., 1991) considered *A. p. oviceps*, which occurs in the Gulf of Mexico from St. Marks River, Florida, to Campeche Bank, Mexico. A study from northwest Florida (Dutka-Gianelli and Murie, 2001) looked at both subspecies (84% *A. a. probatocephalus* and 11% *A. a. oviceps*) and found no significant differences in growth. Anderson et al. (2008) concluded that molecular genetic data indicated a very limited genetic subdivision between the subspecies, despite considerable divergence in some morphological characters.

In contrast, recent analyses of 24 species-specific microsatellite DNA loci of both *A. probatocephalus* subspecies from the Atlantic (Florida to North Carolina) and the Gulf of Mexico (Florida and Texas), showed a

genetic break at the site of the subspecies boundary at Apalachee Bay, Florida (Seyoum et al., in press). These recent genetics results, coupled with the known morphological differences between *A. p. probatocaphalus* and *A. p. oviceps*, support the validity of the 2 subspecies of sheepshead within its U.S. range (Caldwell, 1965), but further study is necessary to better understand processes that contribute to the genetic and morphological differences between these subspecies. A comparison of similarly collected age and growth data is necessary to determine the existence and extent of any subspecific differences in growth.

A fishery can modify the population size and age characteristics of a species by selectively removing younger, faster-growing fish (Ricker, 1975), possibly accounting for the larger fish collected in northwest Florida. Dutka-Gianelli and Murie (2001) suggested that because of the lower density of the human population of northwest Florida, sheepshead there may have experienced less long-term fishing mortality than those in Tampa Bay. Sheepshead enter the fishery in Florida waters at ~280 mm FL (~305 mm TL), at approximately the size predicted for age-3 sheepshead in Tampa Bay (Table 4). Predicted sizes at age are similar between sheepshead in Tampa Bay and those in northwest Florida through age 3 (mean difference of 13.2 mm FL), but after that age, sheepshead from northwest Florida consistently are predicted to attain larger sizes at age (mean difference of 52.4 mm FL).

Regional differences in sheepshead growth parameters are apparent, but within Florida waters it is unnecessary to manage sheepshead regionally. Several fishery management actions, including the ban on entangling gear, a minimum size limit, and recreational-bag (15 fish) and commercial-possession (50 fish) limits were enacted for sheepshead in Florida waters during the 1990s. These actions have brought about a decrease in combined landings of sheepshead and an increase in the size of sheepshead landed; transitional spawning potential ratios of sheepshead in Florida have increased since 1996 and, in 2009, were 37% and 29% for the Atlantic and gulf coasts of Florida, respectively (Munyandorero et al.[1]). Further studies, to better define the stock structure and to describe estuary- or stock-specific differences in growth, would be beneficial and help refine the management of sheepshead in Florida waters.

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Feeding habits and dietary overlap of age-0 winter flounder (*Pseudopleuronectes americanus*) and summer flounder (*Paralichthys dentatus*) in southern New England tidal rivers

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Abstract—Age-0 winter flounder (*Pseudopleuronectes americanus*; 20–90 mm in total length [TL]) and summer flounder (*Paralichthys dentatus*; 19–172 mm TL) were collected from the Seekonk and Taunton Rivers (in Rhode Island and Massachusetts, respectively) from May through September during 2009–2015, and stomach content analysis was used to assess diet composition and resource overlap for these species. Winter and summer flounder underwent ontogenetic dietary shifts. Winter flounder <40 mm TL predominantly fed on copepods, transitioning to amphipods, isopods, and bivalves with increasing size. Polychaetes also were consumed frequently by winter flounder, irrespective of size. The principal prey of summer flounder <60 mm TL were mysid shrimp and copepods, whereas sand shrimp (*Crangon septemspinosa*), amphipods, and fish were the dominant prey of larger conspecifics. There was minimal dietary overlap for the flounder species when comparisons were made independent of body size, indicating food niche segregation. For winter and summer flounder of equivalent sizes, however, dietary overlap was inversely related to TL. Moderate to high resource overlap occurred for small winter and summer flounder (<40 mm TL) and was attributed to their mutual reliance on copepods and amphipods. Despite evidence of dietary overlap, it is unlikely that shared prey resources were diminished enough to negatively affect either flounder species.

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The winter flounder (*Pseudopleuronectes americanus*) is a pleuronectid flatfish that inhabits northwest and mid-Atlantic waters from Nova Scotia southward to Maryland (Pereira et al., 1999). Winter flounder have traditionally supported valuable commercial and recreational fisheries within this geographic range, and, in the United States, this species is managed as 3 discrete stocks in the following areas: southern New England and Middle-Atlantic (SNE-MA), Gulf of Maine, and Georges Bank. There are ongoing concerns with respect to the SNE-MA stock complex because populations of winter flounder have decreased precipitously since the early 1980s and have not rebounded over the last 3 decades (NEFSC[1,2]). Although overexploitation was paramount in their initial population decline (NEFSC[2]), other hypotheses have been purported to explain the failed recovery of winter flounder in southern New England (e.g., the Narragansett Bay Estuary in Rhode Island and Massachusetts) (Collie et al., 2008). These hypotheses include a complex suite of abiotic (temperature) and biotic (predation and resource competition) factors that affect the survival of winter flounder during early development (Keller and Klein-MacPhee, 2000; DeLong et al., 2001; Taylor and Collie, 2003a, 2003b).

Coastal populations of winter flounder spawn demersal eggs inside estuaries during the winter and early spring (Pearcy, 1962). Larval winter flounder hatch 14–21 days after spawning and are pelagic for ~60 days (Chambers and Leggett, 1987), after which they metamorphose into benthic juveniles during the late spring and early summer (Pearcy, 1962). By virtue of adults spawning at cold temperatures (2–5°C), pelagic larvae benefit from reduced competition with other species (Jeffries and Terceiro, 1985). After metamorphosis, however, inter- and intraspecific competition among juvenile winter flounder may be greatly enhanced (Karlson et al., 2007; Nissling et al., 2007; Złoch and Sapota, 2010; Ustups et al., 2016). For example, juvenile winter flounder are often confined to specific depth ranges, have relatively low mobility, and possess more ob-

[1] NEFSC (Northeast Fisheries Science Center).2011. 52nd Northeast regional stock assessment workshop (52nd SAW) assessment report. U.S. Dep. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 11-17, 962 p. [Available from website.]

[2] NEFSC (Northeast Fisheries Science Center). 2015. Operational assessment of 20 Northeast groundfish stocks, updated through 2014. U.S. Dep. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 15-24, 251 p. [Available from website.]

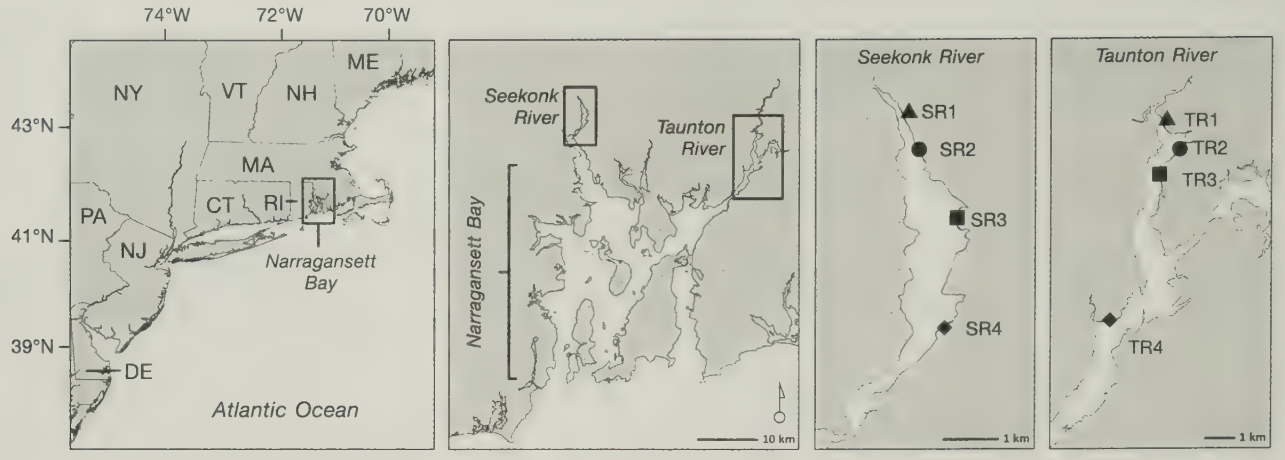

Figure 1

Map of the Seekonk River (SR) and Taunton River (TR), in Rhode Island and Massachusetts, respectively, with points denoting collection sites for age-0 winter flounder (*Pseudopleuronectes americanus*) and summer flounder (*Paralichthys dentatus*). Four sites were sampled fortnightly in each river (SR1–SR4; TR1–TR4) from May through September 2009–2015, with the exception of SR1, which was not surveyed in 2014, and SR3 and TR3, which were not surveyed in 2012–2015.

vious habitat requirements than pelagic fish (Bailey, 1994). The transition in habitat use after metamorphosis and subsequent changes in biotic interactions may be critical in determining their recruitment success and year-class strength.

The summer flounder (*Paralichthys dentatus*) is a paralichthid flatfish that supports lucrative fisheries throughout its geographic range; adults mainly occupy estuarine and inner continental shelf waters in the Mid-Atlantic Bight from Massachusetts to North Carolina (Packer et al., 1999). Summer flounder spawn pelagic eggs on the continental shelf during the fall and early winter, and peak spawning activity occurs in October and November (Packer et al., 1999). Eggs of summer flounder hatch ~3 days after spawning, after which planktonic larvae recruit to inshore nurseries from October through May and subsequently transition to the benthic juvenile life stage.

The distribution of juvenile summer flounder reportedly was limited to inshore nurseries between New Jersey and North Carolina (Able and Kaiser[3])—a range that was delineated at its northern extent by the increased sensitivity of early-stage summer flounder to cold water temperatures (<2°C; Malloy and Targett, 1991). Taylor et al. (2016), however, recently documented a northward shift in the distribution of juvenile (age-0) summer flounder and their use of southern New England nurseries, including the Narragansett Bay and associated tidal rivers. Juvenile summer flounder, therefore, have a geographic range that extends farther north than previously recognized. Moreover, the northward expansion of juvenile summer flounder is attributed to elevated coastal water temperatures in the northwest Atlantic (Smith et al., 2010; Taylor et al., 2016), where warmer temperatures affect the distribution of the adult spawning stock (Nye et al., 2009) and overwintering survival of age-0 summer flounder spawned the previous fall (Malloy and Targett, 1991).

The increased abundance of juvenile summer flounder in southern New England nurseries may have important consequences for resident populations of winter flounder. Foremost, the spatial and temporal overlap of species could increase interspecific dietary overlap and potential competitive interactions in New England coastal habitats (e.g., tidal rivers) (Taylor et al., 2016). To date, the diet composition and foraging ecology of juvenile winter and summer flounder has not been examined in this geographic area or habitat-type. Therefore, the main objective of this study was to evaluate the feeding habits and putative biotic interactions between age-0 winter and summer flounder collected from the Seekonk and Taunton Rivers (in Rhode Island and Massachusetts, respectively): 2 tidal rivers that are contiguous with Narragansett Bay and serve as important nursery habitat for both species (Taylor et al., 2016). Conventional stomach-content analysis was used to explore ontogenetic and spatiotemporal variations in intraspecific diet composition and foraging ecology. Direct visual analysis of food habits and complementary diet indices were also used to assess the extent of dietary overlap of the focal species.

Materials and methods

Field sampling

Age-0 winter flounder and summer flounder were collected from May through September during 2009–2015 from the Seekonk and Taunton Rivers (Fig. 1). Each

[3] Able, K. W., and S. C. Kaiser. 1994. Synthesis of summer flounder habitat parameters. NOAA Coast. Ocean Program, Decis. Anal. Ser. 1, 68 p. NOAA Coastal Ocean Office, Silver Spring, MD.

Table 1

Summary of environmental and biological characteristics at individual sites in the Seekonk River (SR) and Taunton River (TR) in Rhode Island and Massachusetts, respectively, where winter flounder (*Pseudopleuronectes americanus*) and summer flounder (*Paralichthys dentatus*) were collected during 2009–2015. Values represent annual means, with standard errors (SEs), and ranges of measurements taken per sampling effort across months (May–September). Environmental data include water temperature (°C), salinity, and dissolved oxygen (mg/L), and biological data include abundance (individuals/100 m^2) and "fresh" (i.e., measured immediately after capture) total length (mm) of winter flounder (WF) and summer flounder (SF).

	Seekonk River				Taunton River			
Site	SR1	SR2	SR3	SR4	TR1	TR2	TR3	TR4
Environmental characteristics								
Temperature								
Mean	22.9 (SE 1.1)	23.5 (SE 1.2)	23.6 (SE 1.3)	23.2 (SE 1.1)	23.0 (SE 1.3)	23.5 (SE 1.4)	22.8 (SE 1.5)	22.9 (SE 1.4)
Range	19.0–26.8	19.5–27.8	17.6–28.4	19.4–26.8	17.8–26.8	18.1–26.9	17.9–24.9	17.7–26.5
Salinity								
Mean	5.0 (SE 1.3)	7.2 (SE 1.7)	8.3 (SE 1.5)	10.7 (SE 2.0)	3.2 (SE 1.1)	8.9 (SE 1.7)	7.4 (SE 1.3)	19.5 (SE 1.6)
Range	1.7–10.6	2.8–13.8	3.3–14.1	4.3–18.0	0.3–7.4	3.6–15.6	4.2–10.2	12.3–24.0
Dissolved oxygen								
Mean	7.2 (SE 0.8)	7.5 (SE 0.7)	8.8 (SE 1.0)	8.5 (SE 0.8)	6.5 (SE 0.5)	7.1 (SE 0.6)	7.7 (SE 0.6)	6.8 (SE 0.6)
Range	4.4–9.9	4.7–9.7	5.0–12.3	5.9–10.9	4.7–8.1	5.2–9.7	6.3–9.1	4.8–9.1
Biological characteristics								
WF abundance								
Mean	92.4 (SE 44.4)	42.8 (SE 22.2)	6.8 (SE 4.2)	16.2 (SE 5.8)	1.6 (SE 0.7)	5.1 (SE 2.3)	2.4 (SE 0.3)	7.3 (SE 3.0)
Range	5.6–286.1	2.4–136.2	0.0–26.8	4.8–42.4	0.06–4.3	1.2–16.5	2.0–3.4	1.5–21.8
WF total length								
Mean	52.6 (SE 4.7)	49.7 (SE 3.9)	49.2 (SE 3.3)	54.5 (SE 3.0)	64.5 (SE 3.4)	52.7 (SE 4.5)	55.2 (SE 5.0)	53.9 (SE 2.5)
Range	26.9–85.0	26.4–76.3	34.8–70.2	32.8–75.0	23.0–87.0	28.4–77.2	27.5–85.2	37.8–70.8
SF abundance								
Mean	10.5 (SE 4.7)	5.7 (SE 3.6)	5.5 (SE 3.8)	3.2 (SE 2.2)	1.0 (SE 0.6)	2.1 (SE 1.2)	1.7 (SE 0.7)	0.05 (SE 0.04)
Range	1.7–33.2	0.08–24.5	0.0–23.6	0.06–14.3	0.2–3.8	0.1–7.8	0.3–2.8	0.0–0.3
SF total length								
Mean	80.4 (SE 12.0)	84.3 (SE 13.3)	65.7 (SE 3.6)	77.7 (SE 11.2)	88.9 (SE 14.9)	91.1 (SE 12.1)	97.8 (SE 6.9)	105.2 (SE 12.0)
Range	31.1–155.0	32.2–160.0	47.7–71.0	32.0–133.0	37.0–137.0	40.3–236.0	75.4–126.0	69.0–118.9

year, 3–4 sites per river were sampled fortnightly with a beach-seine set that was 15×1.8 m in width (and had 0.64-cm mesh size and 0.48-cm mesh size in the bunt). Sampling occurred during daylight (~0800–1600; ± 2 h of low tide), and 1 haul was conducted per site per date. Winter and summer flounder captured during field sampling were counted immediately (number per 100 square meters; Taylor et al., 2016) and measured to the nearest millimeter for "fresh" total length (TL) (Table 1, Fig. 2). For each sampling effort, ≤10 individuals of each flounder species in a random subsample were preserved in 70% ethanol for subsequent stomach content analysis, and remaining individuals were returned to their place of capture. Surface temperature (degrees Celsius), salinity, and dissolved oxygen (milligrams per liter) were also measured at each site per date with a handheld YSI Model 85[4] meter (YSI Inc., Yellow Springs, OH). The environmental conditions and biological data for winter and summer flounder across the sampling sites are summarized in Table 1.

Stomach content analysis

In the laboratory, winter and summer flounder previously preserved in 70% ethanol were measured for "preserved" TL (in millimeters). Prey were then extracted from fish stomachs and identified to the lowest practical taxon by using stereoscopic microscopes. The contribution of each prey taxon to the diet of winter and summer flounder was expressed by 3 component indices (Hyslop, 1980): frequency of occurrence (*%F*), volumetric percentage (*%V*), and numeric percentage (*%N*), where *%F* equaled the number of stomachs containing a specific prey taxon divided by the total number of stomachs with food contents (a nonadditive index), *%V* was the visual determination of the volumetric contribution of a prey taxon to the total stomach volume of a winter or summer flounder, and *%N* was the number of individuals within a prey taxon divided by the total number of prey identified in a stomach of a winter or summer flounder.

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

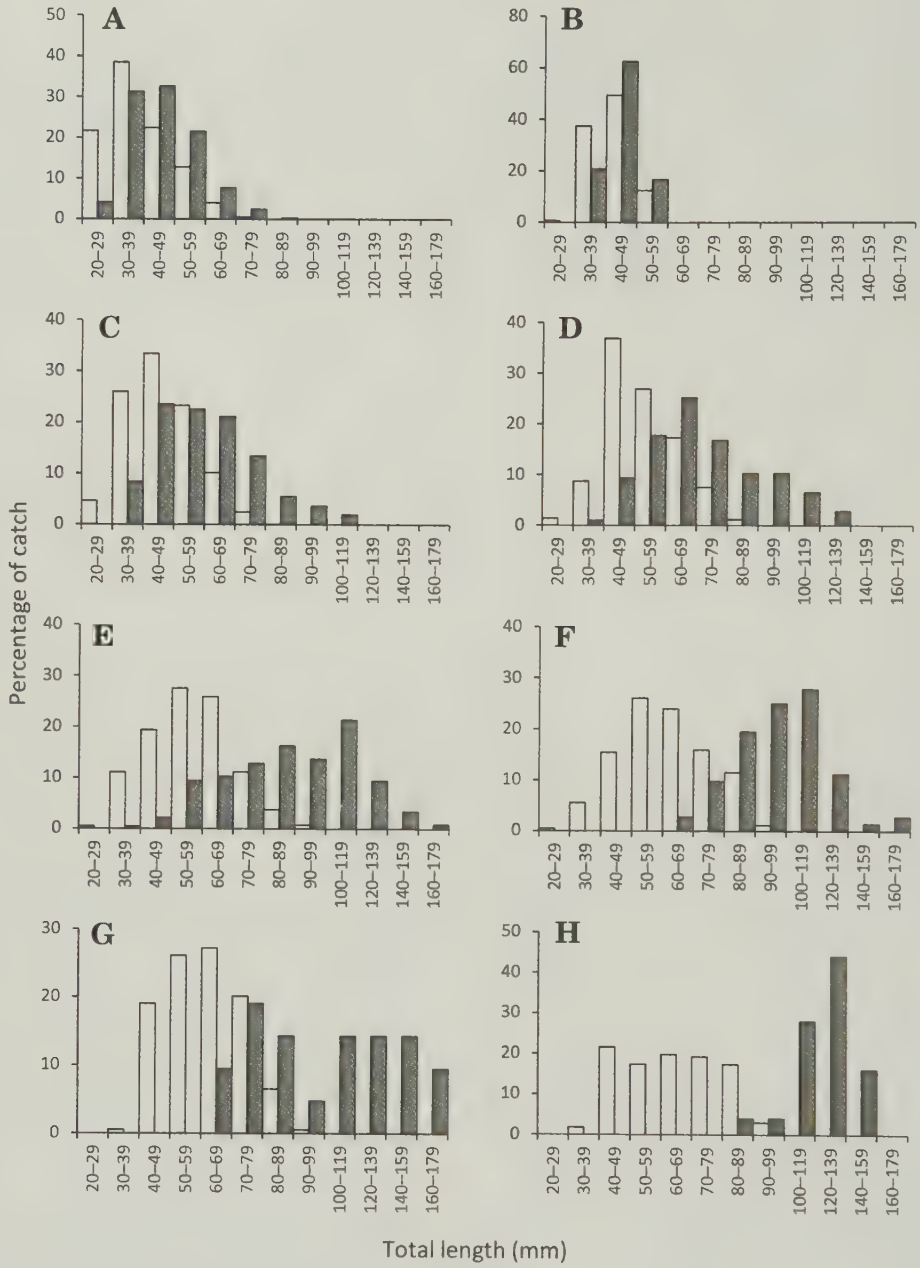

Figure 2

Monthly length–frequency distributions of winter flounder (*Pseudopleuronectes americanus*), indicated with white bars, and summer flounder (*Paralichthys dentatus*), indicated with gray bars, collected from the Seekonk River in (**A**) May, (**C**) June, (**E**) July, and (**G**) August–September and in the Taunton River in (**B**) May, (**D**) June, (**F**) July, and (**H**) August–September. Lengths are "fresh" total lengths (i.e., measured immediately after capture), and catches were compiled across the years 2009–2015.

It is important to note that numerical counts are potentially problematic for soft-bodied prey because mastication of one dietary item could result in multiple countable parts. Accordingly, for soft-body prey, conservative estimates of *%N* were made by counting distinct body features (e.g., counts for polychaetes were typically limited to head and posterior segments, including distinctive tentacles, palps, proboscises, jaws, or cirri). Moreover, when present in the stomach of a winter or summer flounder, a numerical count of 1 was recorded for food items that occurred in nondiscrete units (i.e., detritus; Hyslop, 1980).

The percent index of relative importance (*%IRI*) was used to estimate the overall contribution of a prey taxon to the diet of winter and summer flounder, such that

$$\%IRI_k = \frac{IRI_k}{\sum_{k=1}^{n_p} IRI_k} \times 100, \quad (1)$$

where $\%IRI_k$ = a compound index calculated for prey taxon k and equal to $(\%N_k+\%V_k)\times\%F_k$; and
n_p = the total number of prey taxa identified in stomachs of winter and summer flounder (n_p: 33 and 32, respectively).

The *IRI* index was selected as a descriptor of the diet of winter and summer flounder in this study for 2 principal reasons: 1) to minimize biases associated with individual component indices (Hyslop, 1980; Cortés, 1997; Liao et al., 2001; Hart et al., 2002), although others have noted that compound indices may exacerbate the error term and are affected by the taxonomic resolution of prey (Hyslop 1980; Hansson, 1998), and 2) to facilitate comparisons with other studies of juvenile flounder diet that have a similar approach (Burke, 1995; Carlson et al., 1997; Grover, 1998; Złoch and Sapota, 2010; Sagarese et al., 2011).

Lastly, each seine haul yielded a cluster of winter and summer flounder, and these individuals likely have increased similarities in diet relative to conspecifics sampled at different sites or dates (Bogstad et al., 1995). As such, the aforementioned component and compound diet indices (by percentages) were recalculated by using a cluster sampling estimator (Buckel et al., 1999; Latour et al., 2008), and these data were used in all subsequent analyses (e.g., hierarchical cluster and permutational multivariate analyses; see "Intraspecific dietary analysis" section). The cluster sampling estimator is represented as

$$\%X_k = \frac{\sum_{i=1}^{n_c} M_i q_{ik}}{\sum_{i=1}^{n_c} M_i} \times 100, \quad (2)$$

where $q_{ik} = \frac{x_{ik}}{x_i}$,
$\%X_k$ = one of several diet indices (*%F*, *%N*, *%V*, or *%IRI*) for prey taxon k;
n_c = the number of clusters (e.g., number of seine hauls containing winter or summer flounder);
M_i = the number of winter or summer flounder collected from site i on a specific date;
x_i = the total frequency, number, volume, or index of relative importance of all prey in the stomachs of winter or summer flounder collected from site i; and
x_{ik} = the total frequency, number, volume, or index of relative importance of prey taxon k in flounder stomachs from site i.

The variance estimate for $\%X_k$ was calculated as

$$\mathrm{var}(\%X_k) = \frac{1}{n_c \overline{M}^2} \frac{\sum_{i=1}^{n_c} M_i^2 (q_{ik} - X_k)^2}{n_c - 1} \times 100^2, \quad (3)$$

where $\overline{M} = \frac{\sum_{i=1}^{n_c} M_i}{n_c}$ and represents the average number of winter or summer flounder collected at site i.

Intraspecific dietary analysis

Hierarchical cluster analyses of *%IRI* data were used to examine the diet composition of winter flounder and summer flounder as a function of body size (TL in millimeters). Winter and summer flounder used in the diet study ranged from 20 to 90 mm TL and from 19 to 172 mm TL, respectively (preserved lengths). To assess the effect of fish size on diet, before cluster analyses, winter and summer flounder were grouped into 5-mm-TL and 10-mm-TL size-class intervals, respectively, and *%IRI* was recalculated with Equation 2 (i.e., 1 seine haul produced more than 1 cluster when multiple size classes were present). The statistical software package PRIMER 7.0 (PRIMER-E Ltd., Plymouth, UK) was used to create resemblance matrices of the diet data. For each flounder species, diet data were first log-transformed ($\log[x+1]$) to account for log-normal distributions (Latour et al., 2008), and the Bray-Curtis index was then used to construct a similarity matrix.

Cluster analyses were conducted on the resulting resemblance matrices by using a similarity profiling routine (SIMPROF), which defines statistically distinct groupings among samples (Clarke et al., 2014). Dendrograms derived from cluster analyses were used to visually represent the dietary similarities among size classes of winter and summer flounder (group average method), and similarity percentage analyses (SIMPER) were used to identify the prey taxa that accounted for the dietary similarities or differences within or among groupings. Accordingly, the hierarchical cluster analyses yielded 4 distinct groups of winter and summer flounder (Fig. 3), corresponding to 4 broad size categories. For winter flounder, the size categories were ≤39 mm TL (small), 40–59 mm TL (small–medium), 60–79 mm TL (medium–large), and ≥80 mm TL (large), and, for summer flounder, the categories were ≤59 mm TL (small), 60–79 mm TL (small–medium), 80–119 mm TL (medium–large), and ≥120 mm TL (large).

Spatial (site) and temporal (monthly) variations in diet of winter and summer flounder within each riverine system were examined by using 2-way permutational multivariate analysis of variance (PERMANOVA) models, as provided in the PRIMER 7.0 software package (Anderson et al., 2008). Bray-Curtis resemblance matrices of $\log(x+1)$-transformed data were created by using the previously described methods; however, *%IRI* was recalculated from Equation 2 by grouping winter and summer flounder into their respective broad size categories (4 size categories for each species; Fig. 3). Therefore, each element in a resemblance matrix represented the mean *%IRI* for winter or summer flounder as a function of its size category (small, small–medium, medium–large, and large), site (Seekonk River site 1–4 [SR1–SR4] or Taunton River site 1-4 [TR1–TR4]; Fig. 1), and month (May, June, July, and August–

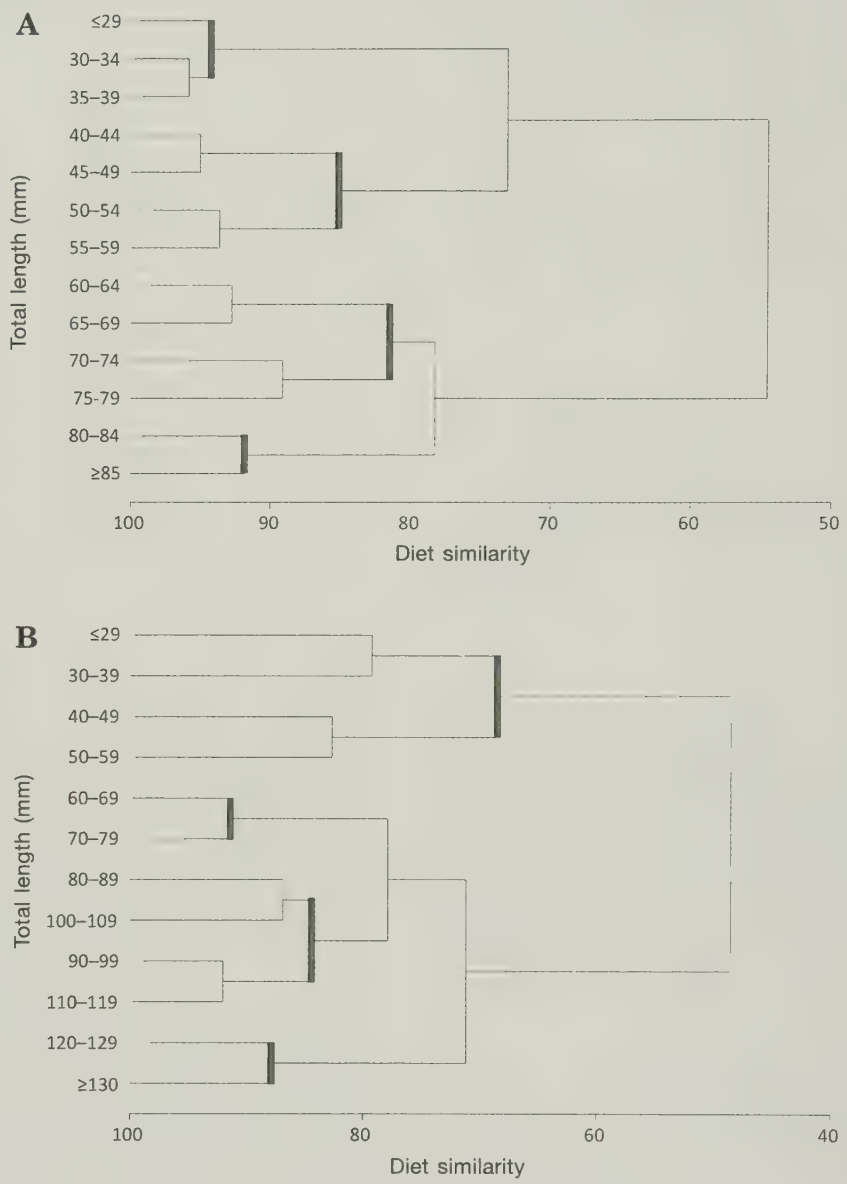

Figure 3

Dendrograms derived from hierarchical cluster analyses and that represent the dietary similarities of (**A**) winter flounder (*Pseudopleuronectes americanus*) and (**B**) summer flounder (*Paralichthys dentatus*) across 5-mm or 10-mm increments of "preserved" total length (i.e., measured in the laboratory after specimens were preserved in 70% ethanol). Vertical gray bars represent distinct dietary groups determined from cluster analyses and similarity profiling. Winter and summer flounder were collected from the Seekonk and Taunton Rivers during 2009–2015.

September). Interannual variations in diet (2009–2015) were excluded from these analyses because some sites were not consistently sampled across years (i.e., SR1, SR3, and TR3).

If significant results ($P<0.05$) were obtained with the PERMANOVA models, SIMPER analyses were conducted to determine which prey taxa contributed to the observed differences in diet of winter and summer flounder across sites or months. Further, to aid in the interpretation of the PERMANOVA results, principal coordinate analysis (PCO) was used to visualize the diet composition data. This method provides a direct projection of data points in space according to their actual dissimilarities, and PCO axes quantify the amount of variation inherent in the resemblance matrix that is attributable to each successive PCO axis (expressed as

a percentage of total variation) (Anderson et al., 2008). Moreover, by using Pearson correlations, vectors of the dominant prey taxa (*%IRI*>1.8%) were superimposed onto the PCO biplots, which correspond to the monotonic relationships between the dietary importance of a prey and the PCO axes (Anderson et al., 2008).

Diet diversity for winter and summer flounder was estimated by using the Levins index of niche breadth (*B*) (Levins, 1968), such that

$$B = \frac{1}{n_p - 1}\left(\frac{1}{\sum_{k=1}^{n_p} P_k^2} - 1\right), \quad (4)$$

where B = the standardized index of niche breadth for winter or summer flounder;
P_k = the proportional contribution of prey taxon k to the diet of a flounder species (based on IRI_k); and
n_p = the total number of prey taxa identified in the stomachs of a flounder species.

Values of *B* range between 0 and 1, and a value of 0 indicates maximum dietary specialization and a value of 1 indicates nondiscrimination of prey. Moreover, *B*>0.6 denotes a high niche breadth, whereas values of 0.4–0.6 and <0.4 represent moderate and low diet diversity, respectively (Novakowski et al., 2008). In this study, *B* was calculated for winter and summer flounder irrespective of their body sizes (the size-independent estimate) and at specific size classes (the size-dependent estimate). For the latter, for each sampling site, *B* was estimated for winter and summer flounder at 5-mm TL and 10-mm TL size-class intervals, respectively. Nonlinear (exponential) regression models were used to examine the effect of body size of winter and summer flounder on diet diversity.

Interspecific dietary overlap

The extent of dietary overlap between winter flounder and summer flounder was evaluated by using 2 approaches. First, after the procedures described above, 2-way PERMANOVA models, PCO biplots, and SIMPER analyses were used to examine similarities in diet composition as a function of species type (winter or summer flounder) and size categorization (small, small–medium, medium–large, or large). Second, the Schoener index was used to assess interspecific dietary overlap (Schoener, 1970), such that

$$\alpha = 1 - 0.5\left(\sum_{k=1}^{n_p} | P_{hk} - P_{jk} \right), \quad (5)$$

where α estimates the degree of resource overlap between flounder species; and
P_{hk} and P_{jk} = the proportional contributions of prey taxon k (based on IRI_k) to the diet of winter flounder (h) and summer flounder (j), respectively.

The result is an α value that ranges between 0 and 1, and α>0.6 denotes biologically significant overlap in the use of prey resources (Schoener, 1970), whereas values of 0.4–0.6 and <0.4 represent moderate and low dietary overlap, respectively (Hartman and Brandt, 1995; Novakowski et al., 2008; Zahn Seegert et al., 2014). In this study, the Schoener index was calculated for winter and summer flounder irrespective of their body sizes (size-independent estimate) and for winter and summer flounder of equivalent sizes (size-dependent estimates). For the latter, for each sampling site, α was evaluated for winter and summer flounder at 5-mm-TL increments ranging from 20 to 90 mm TL (14 total increments). A nonlinear (logarithmic) regression model was used to examine the effect of fish body size on the extent of dietary overlap.

Results

Intraspecific diet composition and diversity

During 2009–2015, winter flounder and summer flounder were collected from 186 and 132 seine hauls, respectively, in the Seekonk and Taunton Rivers (Table 2). The stomachs of 1109 winter flounder and 749 summer flounder were examined in total, of which 89.8% and 95.3% contained prey. In stomachs of winter flounder, 33 unique prey taxa were identified (mean number of prey taxa per stomach: 3.0 [standard error (SE)] 0.04) (Table 2). The dominant prey of winter flounder, with respect to the *%IRI*, were amphipods, harpacticoid and calanoid copepods, polychaetes, bivalves (e.g., clam siphons), insects (e.g., chironomid larvae), and isopods (Table 2). Collectively, these taxa accounted for 98.8% of the relative diet of winter flounder 20–90 mm TL. Other prey that were of lesser dietary importance, yet relatively common in stomachs of winter flounder (*%F*>1%), included ostracods, nematodes, and mysid shrimp. Summer flounder 19–172 mm TL consumed 32 different prey taxa and each stomach contained, on average, 2.1 (SE 0.03) prey taxa (Table 2). Five prey taxa composed 98.9% of the diet of summer flounder (based on *%IRI*): mysid shrimp, sand shrimp, amphipods, fish, and copepods (Table 2). Other prey encountered at relatively high frequencies in stomachs of summer flounder (*%F*>1%) were polychaetes, cumaceans, clam siphons, and ostracods.

According to the niche breadth index, a low level of diet diversity was observed for both winter and summer flounder when calculations were made irrespective of body size (*B*: 0.24 and 0.30; Table 2). Niche dietary breadth of winter and summer flounder, however, significantly expanded with increasing body lengths (exponential regression: winter flounder, F=11.05, coefficient of determination [r^2]=0.104, P<0.005; summer flounder, F=6.61, r^2=0.09, P<0.05) (Fig. 4, A and B). Specifically, winter flounder had a moderate and high degree of diet diversity when individuals exceeded ~75 mm TL (*B*≥0.4), and this broader-based diet was most evident in the Taunton River (Fig. 4A). For summer flounder,

Table 2

Contributions of prey taxa to the diets of winter flounder (*Pseudopleuronectes americanus*) and summer flounder (*Paralichthys dentatus*) expressed as frequency of occurrence (*%F*), numeric percentage (*%N*), volumetric percentage (*%V*), and the index of relative importance (*%IRI*, Eq. 1). Mean values (and standard errors [SEs]) were calculated by using a cluster sampling estimator (Eqs. 2 and 3). Size-independent estimates of Levins niche breadth index (*B*; Eq. 4) and Schoener dietary overlap index (α; Eq. 5) are also presented. Winter and summer flounder were collected from the Seekonk and Taunton Rivers during 2009–2015.

	Winter flounder				Summer flounder			
Prey taxon	*%F*	*%N*	*%V*	*%IRI*	*%F*	*%N*	*%V*	*%IRI*
Crustaceans								
Amphipoda (amphipod)	81.2 (SE 0.3)	27.9 (SE 0.3)	47.7 (SE 0.3)	48.3 (SE 0.3)	41.9 (SE 0.4)	14.8 (SE 0.3)	15.6 (SE 0.2)	15.0 (SE 0.3)
Isopoda (isopod)								
Anthuridae (anthurid isopod)	8.4 (SE 0.3)	1.3 (SE 0.1)	2.3 (SE 0.1)	1.3 (SE 0.1)	–	–	–	–
Idoteidae (idoteid isopod)	3.4 (SE 0.1)	0.4 (SE 0.01)	0.7 (SE 0.03)	0.4 (SE 0.02)	0.2 (SE 0.02)	<0.1	0.2 (SE 0.01)	<0.1
Tanaidacea (tanaid)	–	–	–	–	0.3 (SE 0.02)	<0.1	<0.1	<0.1
Cumacea (cumacean)	0.3 (SE 0.08)	< 0.1	< 0.1	< 0.1	1.8 (SE 0.1)	0.3 (SE 0.01)	0.4 (SE 0.02)	0.2 (SE 0.02)
Calanoida/Harpacticoida (copepod)	66.4 (SE 0.4)	44.5 (SE 0.4)	19.4 (SE 0.2)	25.6 (SE 0.3)	14.5 (SE 0.3)	15.5 (SE 0.5)	3.7 (SE 0.1)	4.0 (SE 0.1)
Ostracoda (ostracod)	8.9 (SE 0.2)	0.6 (SE 0.01)	0.4 (SE 0.01)	0.1 (SE 0.01)	1.1 (SE 0.1)	0.2 (SE 0.01)	<0.1	<0.1
Mysidacea (mysid shrimp)	1.3 (SE 0.1)	< 0.1	0.2 (SE 0.01)	0.1 (SE 0.01)	70.8 (SE 0.5)	51.6 (SE 0.5)	49.1 (SE 0.6)	54.4 (SE 0.6)
Decapoda (decapod)								
Crangon septemspinosa (sand shrimp)	< 0.1	< 0.1	< 0.1	< 0.1	29.6 (SE 0.5)	10.4 (SE 0.2)	20.1 (SE 0.4)	18.6 (SE 0.4)
Palaemonidae (grass shrimp)	–	–	–	–	0.1 (SE 0.01)	<0.1	0.1 (SE 0.01)	<0.1
Callinectes sapidus (blue crab)	–	–	–	–	0.2 (SE 0.01)	<0.1	<0.1	<0.1
Grapsidae or Xanthidae (shore or mud crab)	0.8 (SE 0.03)	0.3 (SE 0.01)	0.4 (SE 0.01)	0.3 (SE 0.01)	0.8 (SE 0.03)	0.2 (SE 0.01)	0.4 (SE 0.01)	0.2 (SE 0.01)
Pagurus longicarpus (longwrist hermit)	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified crab (zoea life stage)	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified crab (megalope life stage)	0.9 (SE 0.03)	0.3 (SE 0.01)	0.2 (SE 0.01)	0.2 (SE 0.01)	0.2 (SE 0.01)	<0.1	<0.1	<0.1
Unidentified crustacean	0.3 (SE 0.02)	<0.1	<0.1	<0.1	0.2 (SE 0.01)	0.1 (SE 0.01)	<0.1	<0.1
Insects								
Chironomidae (midge larvae)	22.8 (SE 0.5)	6.9 (SE 0.2)	8.9 (SE 0.2)	6.3 (SE 0.2)	0.2 (SE 0.01)	<0.1	<0.1	<0.1
Coleoptera (beetle)	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Diptera (pupae life stage)	<0.1	<0.1	<0.1	<0.1	0.4 (SE 0.03)	<0.1	0.1 (SE 0.01)	<0.1
Formicidae (ant)	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified insect	<0.1	<0.1	<0.1	<0.1	0.7 (SE 0.05)	0.1 (SE 0.01)	<0.1	<0.1
Arachnids								
Acarina (mite)	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Aranae (spider)	–	–	–	–	0.1 (SE 0.01)	<0.1	<0.1	<0.1

Table continued

niche dietary breadth was more variable across lengths and riverine sites, and moderate and high diet diversity was common for summer flounder >115 mm TL (Fig. 4B).

Ontogenetic effects on intraspecific diets

Hierarchical cluster analyses revealed distinct dietary groups for winter flounder and summer flounder, and these groups corresponded with 4 broad size categories for each species (Fig. 3). After accounting for the size-dependent effects on diet, the corrected cluster sample sizes for winter and summer flounder (n_c) equaled 242 and 157, respectively (i.e., 1 seine haul resulted in >1 cluster when multiple size classes were present). Small winter flounder (≤39 mm TL) had a 94.9% similarity in diet (SIMPROF: π=0.16, P=0.83; Fig. 3A) and fed predominantly on copepods (*%IRI*=76.5%), polychaetes (*%IRI*=11.8%; unidentified and *Fabricia sabella*), and amphipods (*%IRI*=11.4%) (Fig. 5A). Winter flounder

Table 2 (*Continued*)

	Winter flounder				Summer flounder			
Prey taxon	*%F*	*%N*	*%V*	*%IRI*	*%F*	*%N*	*%V*	*%IRI*
Worms								
Polychaeta (polychaete)								
Ampharetidae								
(ampharetid worm)	1.9 (SE 0.04)	0.3 (SE 0.01)	0.6 (SE 0.01)	0.2 (SE 0.01)	0.1 (SE 0.01)	<0.1	<0.1	<0.1
Fabricia sabella (fan worm)	8.6 (SE 0.2)	2.8 (SE 0.1)	1.9 (SE 0.1)	1.6 (SE 0.1)	0.2 (SE 0.04)	<0.1	<0.1	<0.1
Glyceridae (blood worm)	0.1 (SE 0.01)	<0.1	<0.1	<0.1	–	–	–	–
Nereididae (clam worm)	2.1 (SE 0.1)	0.3 (SE 0.01)	0.6 (SE 0.02)	0.2 (SE 0.01)	0.5 (SE 0.03)	<0.1	<0.1	<0.1
Phyllodocidae (paddle worm)	8.0 (SE 0.2)	0.9 (SE 0.02)	1.2 (SE 0.03)	0.6 (SE 0.01)	–	–	–	–
Polydora spp. (mud worm)	4.3 (SE 0.1)	1.4 (SE 0.04)	1.1 (SE 0.03)	0.8 (SE 0.03)	–	–	–	–
Unidentified polychaete	26.6 (SE 0.4)	4.8 (SE 0.1)	8.1 (SE 0.1)	5.8 (SE 0.1)	3.9 (SE 0.1)	0.7 (SE 0.02)	1.0 (SE 0.03)	0.4 (SE 0.02)
Nematoda (nematode)	2.1 (SE 0.1)	0.2 (SE 0.01)	<0.1	<0.1	0.1 (SE 0.01)	<0.1	<0.1	<0.1
Mollusks								
Bivalvia (bivalve)								
Mya arenaria (softshell)	0.1 (SE 0.01)	<0.1	<0.1	<0.1	–	–	–	–
Unidentified clam								
(whole clam)	1.1 (SE 0.03)	0.1 (SE 0.01)	0.2 (SE 0.01)	<0.1	–	–	–	–
Unidentified clam								
(clam siphon)	25.2 (SE 0.4)	6.9 (SE 0.1)	5.4 (SE 0.1)	4.8 (SE 0.1)	1.4 (SE 0.1)	0.2 (SE 0.01)	0.1 (SE 0.01)	<0.1
Gastropoda	0.2 (SE 0.01)	<0.1	<0.1	<0.1	–	–	–	–
Fish								
Anguilla rostrata								
(American eel)	–	–	–	–	0.1 (SE 0.01)	<0.1	<0.1	<0.1
Catostomus commersoni								
(white sucker)	–	–	–	–	0.4 (SE 0.03)	0.2 (SE 0.02)	0.4 (SE 0.03)	0.2 (SE 0.02)
Clupeidae (herring)	–	–	–	–	1.0 (SE 0.04)	0.3 (SE 0.01)	0.7 (SE 0.03)	0.4 (SE 0.02)
Gobiidae (goby)	–	–	–	–	0.1 (SE 0.01)	<0.1	<0.1	<0.1
Menidia menidia								
(Atlantic silverside)	–	–	–	–	0.1 (SE 0.01)	0.1 (SE 0.01)	0.1 (SE 0.01)	0.1 (SE 0.01)
Micropterus salmoides								
(largemouth bass)	–	–	–	–	0.1 (SE 0.01)	<0.1	<0.1	<0.1
Pseudopleuronectes americanus								
(winter flounder)	–	–	–	–	2.4 (SE 0.1)	0.3 (SE 0.01)	1.1 (SE 0.04)	0.4 (SE 0.02)
Syngnathus fuscus								
(northern pipefish)	–	–	–	–	0.3 (SE 0.01)	<0.1	<0.1	<0.1
Unidentified fish	–	–	–	–	8.8 (SE 0.3)	4.7 (SE 0.3)	6.2 (SE 0.3)	5.2 (SE 0.3)
Detritus	0.4 (SE 0.02)	< 0.1	0.3 (SE 0.02)	0.2 (SE 0.01)	0.6 (SE 0.02)	<0.1	0.2 (SE 0.01)	<0.1
Total number of stomachs examined (n_t)			1109			749		
Percentage of empty stomachs (%)			10.2			4.7		
Total number of clusters (seine hauls with winter or summer flounder; n_c)			186			132		
Unique prey per stomach (mean)			3.0 (SE 0.04)			2.1 (SE 0.03)		
Niche breadth index (B)			0.24			0.30		
Dietary overlap index (α)				0.20				

within the small–medium (40–59 mm TL) and medium–large (60–79 mm TL) size categories had 85.1% and 81.4% dietary similarities, respectively (SIMPROF: small–medium, π=2.42, P=0.10; medium–large, π=2.21, P=0.20; Fig. 3A). Consumption of polychaetes remained consistent at these moderate body sizes (*%IRI* ~10–13%; unidentified, *F. sabella*, and *Polydora* spp.), but there was a decreased reliance on copepods (*%IRI* declined from 48.9% to 5.1%) and a greater importance of amphipods (*%IRI* increased from 34.3% to 63.7%) (Fig. 5A). There also was evidence of small–medium and medium–large winter flounder feeding on bivalves, and that feeding was mostly limited to siphon cropping (*%IRI*: 5.9% and 13.7% for small–medium and medium–large size categories, respectively) (Table 2). Large winter flounder (≥80 mm TL) had 91.8% dietary similarity (SIMPROF: π=0.00, P=1.00; Fig. 3A). There was an absence of copepods in the diet of these winter flounder (*%IRI*=0.0%), and amphipods (*%IRI*=51.7%), polychaetes (*%IRI*=22.4%; unidentified and nereidids),

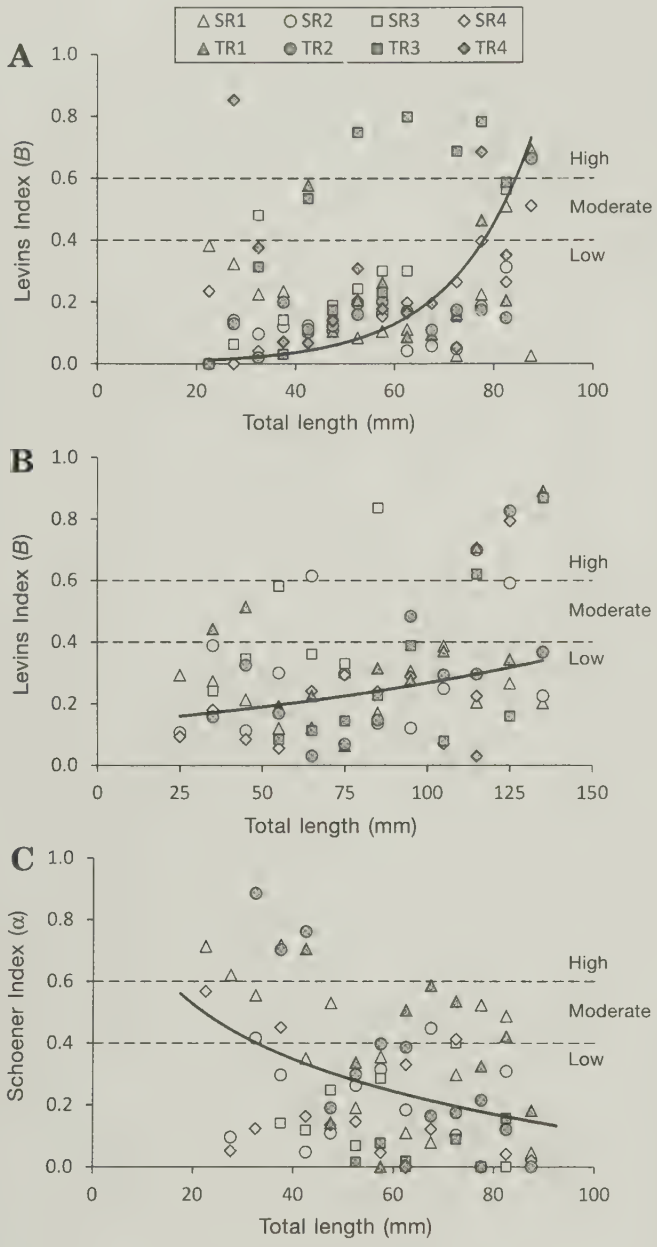

Figure 4

Diet diversity and dietary overlap of winter flounder (*Pseudopleuronectes americanus*) and summer flounder (*Paralichthys dentatus*) as a function of "preserved" total length (i.e., measured in the laboratory after specimens were preserved in 70% ethanol) and riverine site (for locations of sampling sites, see Fig. 1). Diet diversity of (**A**) winter flounder and (**B**) summer flounder was expressed by the Levins index of niche breadth (B; Eq. 4), and horizontal dashed lines differentiate among high (B>0.6), moderate (B=0.4-0.6), and low (B<0.4) niche breadths. (**C**) Dietary overlap is expressed by the Schoener index (α; Eq. 5), and horizontal dashed lines differentiate high (α>0.6), moderate (α=0.4-0.6), and low (α<0.4) overlap. Nonlinear (exponential or logarithmic) regression models were fitted to the data and are represented by the solid lines. Winter and summer flounder were collected from the Seekonk River (SR) and Taunton River (TR) during 2009–2015.

and bivalves (*%IRI*=18.4%) remained important food items (Fig. 5A). The largest winter flounder also consumed isopods and crabs (e.g., megalope) in relatively high proportions (*%IRI*: 3.1% and 4.0%, respectively) (Table 2, Fig. 5A).

Summer flounder within the smallest size category (≤59 mm TL) had 68.2% dietary similarity (SIMPROF: π=1.88, P=0.69; Fig. 3B), with mysid shrimp, copepods, and amphipods representing the most dominant prey (*%IRI*: 59.5%, 22.9%, and 15.1%, respectively), and sand shrimp and fish consigned to secondary importance (*%IRI*≤1.3%) (Fig. 5B). The similarities in diet of summer flounder within the other size classes ranged between 84.2% and 91.3% (SIMPROF: small–medium [60–79 mm TL], π=0.00, P=1.00; medium–large [80–119 mm TL], π=1.25, P=0.63; large [≥120 mm TL], π=0.00, P=1.00; Fig. 3B). Copepods were not observed in the stomachs of moderate- and large-size summer flounder (*%IRI*=0.0%; Fig. 5B). Moreover, progressive increases in size of summer flounder resulted in a decline in the dietary importance of mysid shrimp and amphipods (*%IRI*: mysid shrimp, from 35.6% to 6.4%; amphipods, from 43.7% to 17.5%), whereas sand shrimp and fish became increasingly more dominant (*%IRI*: shrimp, from 19.2% to 66.8%; fish, from 1.0% to 6.0%) (Fig. 5B). Of the identifiable fish remains in the stomachs of summer flounder, winter flounder had the highest *%F* (2.4%) and *%IRI* (0.4%) (Table 2), verifying predator–prey interactions between the focal species.

Spatiotemporal effects on intraspecific diets

Winter flounder diet in the Seekonk and Taunton Rivers varied statistically by site and month (2-way PERMANOVA: site, pseudo-F=3.04–4.77, P<0.01–0.001; month, pseudo-F=4.94–10.07, P<0.001), and the site–month interaction effects were not significant (2-way PERMANOVA: site×month, pseudo-F=0.73–1.77, P=0.06–0.75) (Fig. 6). Principal coordinate analysis revealed that month most closely corresponded with the first PCO axis (PCO1) and accounted for 56.7% and 59.3% of the explainable variation in diet of winter flounder in the Seekonk and Taunton Rivers (Fig. 6, B and D). The second PCO axis (PCO2), in contrast, was best represented by riverine sites (SR1–SR4 or TR1–TR4) and accounted for 20.5–28.8% of the total variation in diet. Differences in diet of winter flounder across months were attributed mainly to the importance of copepods at the onset of this study (from May through August–September, *%IRI* for copepods declined from 61.6% to 0.8%), and copepods were steadily replaced by polychaetes thereafter (from May through August–September, *%IRI* for polychaetes increased from 5.1% to 42.6%) (Fig. 6, A and C).

Moreover, in the Taunton River, winter flounder consumed a high proportion of crab megalope in July and August–September, especially in the middle and upper portions of the river (TR1–TR3, July and August–September *%IRI* for crab: 1.6–39.4%). Spatial differences in the diet of winter flounder from the Taunton River were attributed also to the disproportionate contribution of bivalves and anthurid isopods in the upper reaches of the river (TR1 and TR2 *%IRI*: bivalve=7.4–26.4%; isopod=3.0–12.4%), and polychaetes were dominant at TR4, particularly from mid- to late summer (TR4, July and August–September *%IRI* for polychaetes, mostly unidentified, phyllodocid, and *Polydora* spp., was 52.0–77.4%) (Fig. 6C). In contrast, bivalves and idoteid isopods were important prey in the lower reaches of the Seekonk River (SR3 and SR4 *%IRI*: bivalves=9.1–27.6%; isopod=2.3–6.3%), whereas chironomid larvae were relatively unique to SR2 (SR2 *%IRI* for chironomids: 1.2–20.0%) (Fig. 6A). Amphipods were a broadly used prey resource by winter flounder, but no discernible spatiotemporal patterns in their dietary contribution were evident (Fig. 6).

Summer flounder feeding habits in each river varied temporally (2-way PERMANOVA for month: Seekonk, pseudo-F=5.39, P<0.001; Taunton, pseudo-F=3.86, P<0.002), but dietary differences across sites were evident only in the Taunton River (2-way PERMANOVA for site: Seekonk, pseudo-F=1.90, P=0.08; Taunton, pseudo-F=3.97, P<0.002) (Fig. 7). Further, in each instance, the site–month interaction effect was not significant (2-way PERMANOVA: site×month, pseudo-F=0.50–0.64, P=0.79–0.96). The first and second axes of the PCO biplots were correlated most with month and site, respectively, and accounted for 55.4–66.5% and 14.7–24.3% of the total variation in diet of summer flounder in the Seekonk and Taunton Rivers (Fig. 7, B and D).

The significant temporal variation in diet of summer flounder was attributed to the initial contribution of mysid shrimp and copepods in May–June and subsequent dietary shifts toward amphipods in later months (from May to August–September, *%IRI* decreased for mysid shrimp from 54.8% to 16.2% and for copepods from 10.9% to 0.0% and increased for amphipods from 15.6% to 50.0%) (Fig. 7). The dietary contributions of other important prey taxa, including sand shrimp and fish, varied inconsistently across months. Further, summer flounder collected from the upper reaches of the Taunton River consumed more amphipods and fish than conspecifics from southerly locations (TR1–TR4 *%IRI*: amphipods=47.3% versus 0.0%; fish=8.9% versus 0.0%) (Fig. 7, C and D). Sand shrimp were also overwhelmingly dominant at TR4 in July (*%IRI*=97.5%); however, dietary resolution for this site–month interaction was confounded by small samples sizes (n_c=3).

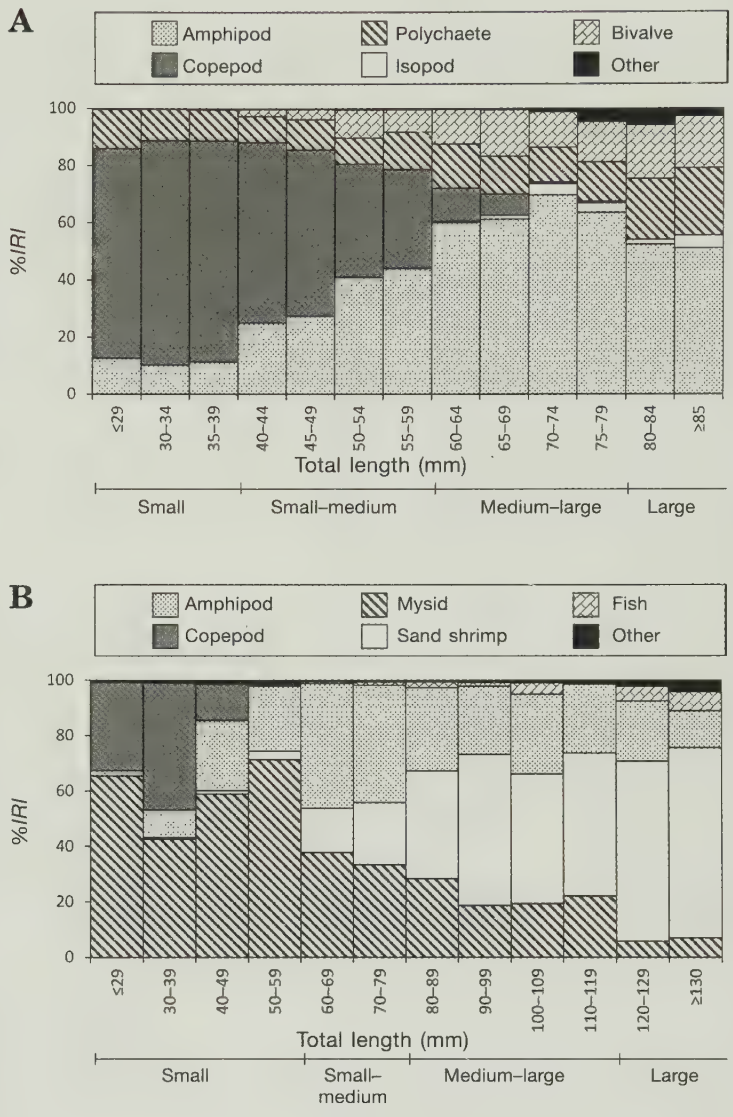

Figure 5

Contributions of prey taxa to the diets of (**A**) winter flounder (*Pseudopleuronectes americanus*) and (**B**) summer flounder (*Paralichthys dentatus*) as a function of "preserved" total length (i.e., measured in the laboratory after specimens were preserved in 70% ethanol). Diet is expressed as an index of relative importance (*%IRI*; Eq. 1), and horizontal brackets represent distinct (size-based) dietary groups determined from hierarchical cluster analyses and similarity profiling (Fig. 3). Winter and summer flounder were collected from the Seekonk and Taunton Rivers during 2009–2015.

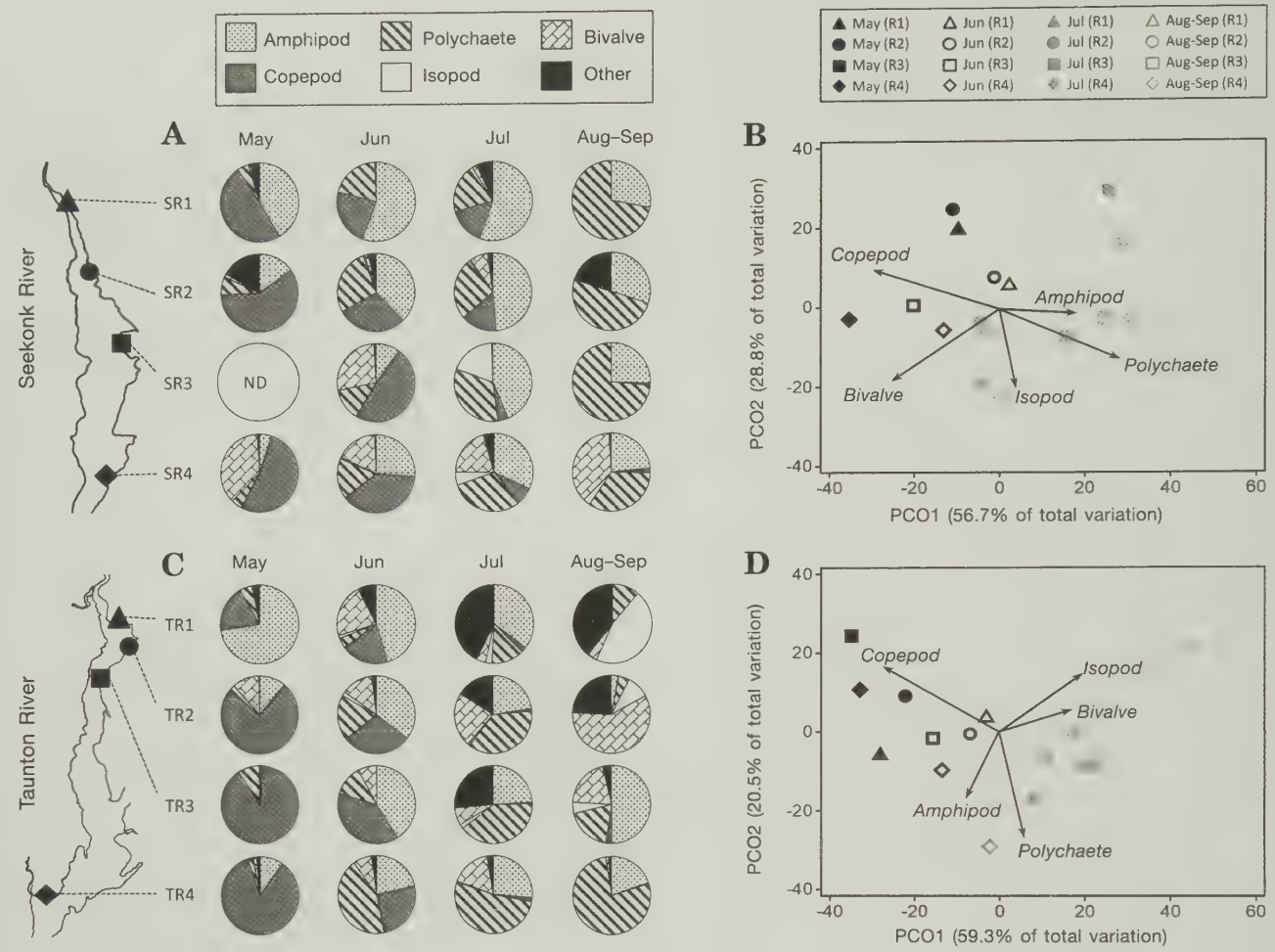

Figure 6

Contributions of prey taxa to the diet of winter flounder (*Pseudopleuronectes americanus*) collected during 2009–2015 in the (**A**, **B**) Seekonk River and (**C**, **D**) Taunton River, as a function of month (May–September) and site (SR1–SR4; TR1–TR4). (**A**, **C**) Dietary contributions of prey are expressed as an index of relative importance, and (**B**, **D**) data points from principal coordinate analysis (PCO) are projected in space according to their actual dissimilarities. Arrows superimposed on the PCO biplots represent vectors of dominant prey taxa, and vectors correspond with the monotonic relationships between the dietary importance of a prey and the PCO axes. The first (PCO1) and second (PCO2) axes correspond with month and site, respectively, and quantify the percentage of total variation in diet of winter flounder. ND signifies no data.

Interspecific dietary overlap

The diet of winter flounder and summer flounder varied as a function of species type and length classification (2-way PERMANOVA: species, pseudo-F=77.80, P<0.001; size, pseudo-F=5.66, P<0.001). The species–size interaction effect also was significant, thereby precluding contrasts across the main effects (2-way PERMANOVA: species×size, pseudo-F=3.02, P<0.001). With respect to interspecific comparisons, SIMPER analyses revealed that dietary similarities were highest among small-size winter and summer flounder (average similarity: 29.4%), and increasing lengths resulted in greater deviations in their respective diets (average similarity among moderate and large winter and summer flounder: 20.3–22.3%). The higher degree of resource overlap among small winter and summer flounder was attributed to their initial feeding on copepods, followed by ontogenetic dietary shifts away from this shared prey item (Figs. 5–7).

Similarities and differences in the diets of winter and summer flounder were re-affirmed by PCO (Fig. 8). Species type most closely corresponded with the PCO1 and accounted for 40.6% of the explainable variation in diet. Conversely, body size of winter and summer flounder explained 14.4% of the total variation in diet and was visually represented by the PCO2. Vectors of the dominant prey taxa were superimposed onto the

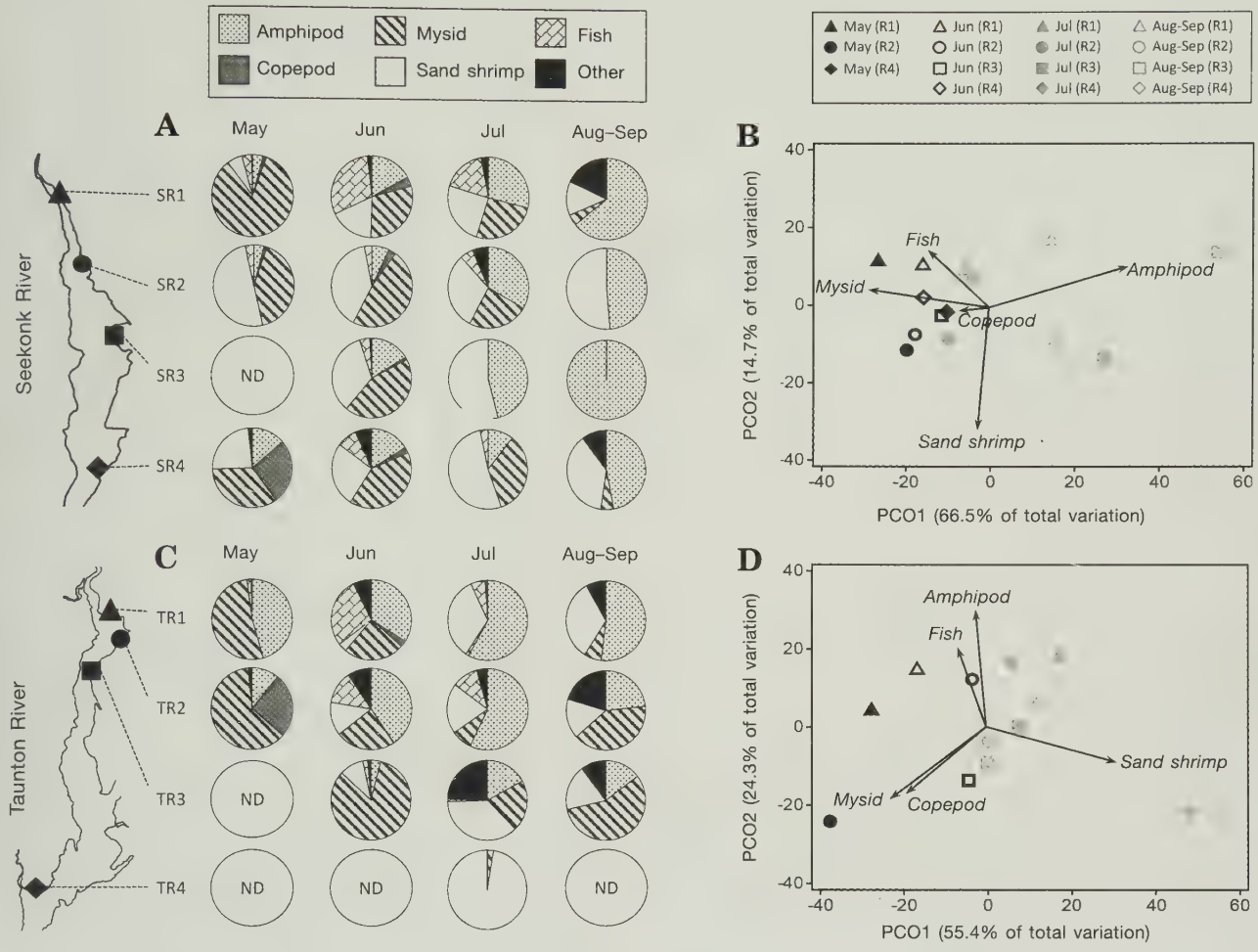

Figure 7

Contributions of prey taxa to the diet of summer flounder (*Paralichthys dentatus*) collected during 2009–2015 in the (**A**, **B**) Seekonk River and (**C**, **D**) Taunton River, as a function of month (May–September) and site (SR1–SR4; TR1–TR4). (**A**, **C**) Dietary contributions of prey are expressed as the index of relative importance, and (**B**, **D**) data points from principal coordinate analysis (PCO) are projected in space according to their actual dissimilarities. Arrows superimposed on the PCO biplots represent vectors of dominant prey taxa, and vectors correspond with the monotonic relationships between the dietary importance of a prey and the PCO axes. The first (PCO1) and second (PCO2) ordination axes correspond with month and site, respectively, and quantify the percentage of total variation in diet of summer flounder. ND signifies no data.

PCO biplots and again verified that copepods and, to a lesser extent, amphipods were shared prey among small and small–medium winter and summer flounder (Fig. 8). Prey vectors also illustrated the positive correlations between winter and summer flounder TL and the discrepancies in their respective diets. For example, although amphipods remained an important prey for both species, moderate- and large-size winter flounder also fed on polychaetes, bivalves, and isopods, whereas sand shrimp and fish became increasingly important to the diet of summer flounder (Fig. 8).

The Schoener index indicated minimal dietary overlap for winter and summer flounder when calculations were made independent of body size (α=0.20; Table 2). For winter and summer flounder of equivalent sizes, however, dietary overlap was inversely related to total length (logarithmic regression: F=13.90, r^2=0.156, P<0.0005) (Fig. 4C). Moderate to high dietary overlap occurred among winter and summer flounder at sizes <40 mm TL ($\alpha \geq 0.4$), and that overlap was due to their mutual reliance on copepods, as described previously (Figs. 5–7). There was also evidence of resource sharing among winter and summer flounder as large as 85 mm TL (Fig. 4C), and that resource sharing was attributed to both species continually feeding on amphipods (Figs. 5–7). There was a spatial component to dietary overlap, as well, such that similarities in the diet composition of winter and summer flounder were most prevalent in

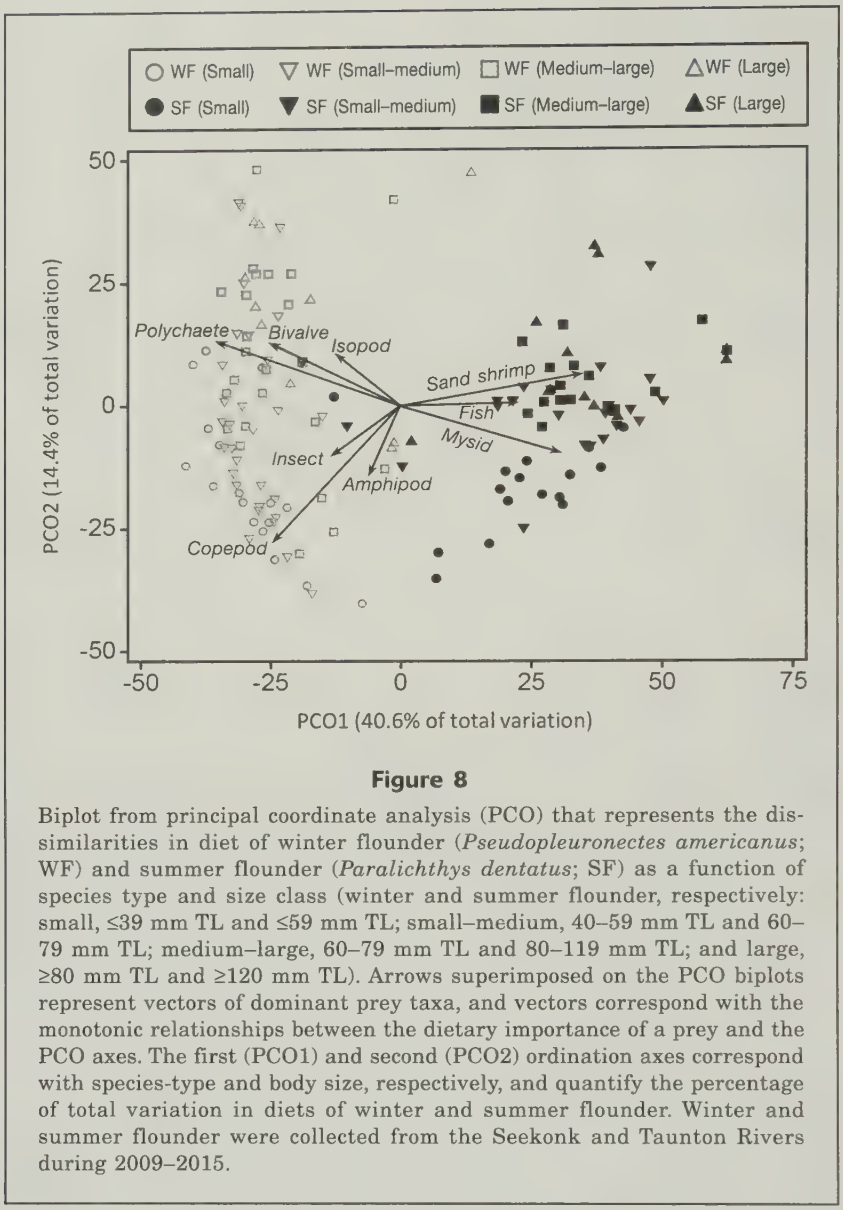

Figure 8

Biplot from principal coordinate analysis (PCO) that represents the dissimilarities in diet of winter flounder (*Pseudopleuronectes americanus*; WF) and summer flounder (*Paralichthys dentatus*; SF) as a function of species type and size class (winter and summer flounder, respectively: small, ≤39 mm TL and ≤59 mm TL; small–medium, 40–59 mm TL and 60–79 mm TL; medium–large, 60–79 mm TL and 80–119 mm TL; and large, ≥80 mm TL and ≥120 mm TL). Arrows superimposed on the PCO biplots represent vectors of dominant prey taxa, and vectors correspond with the monotonic relationships between the dietary importance of a prey and the PCO axes. The first (PCO1) and second (PCO2) ordination axes correspond with species-type and body size, respectively, and quantify the percentage of total variation in diets of winter and summer flounder. Winter and summer flounder were collected from the Seekonk and Taunton Rivers during 2009–2015.

the upper reaches of the Seekonk and Taunton Rivers (SR1–SR2; TR1–TR2) (Fig. 4C).

Discussion

Intraspecific diet composition

This study provides a comprehensive analysis of the diet composition of age-0 winter flounder and summer flounder collected from 2 southern New England tidal rivers. Accordingly, both flounder species from this geographic area and habitat type had a generalist feeding strategy, as determined by the wide variety of prey consumed during the early juvenile life stage (33 and 32 novel prey taxa, respectively). Winter flounder fed predominantly on small crustaceans (e.g., amphipods, copepods, isopods, ostracods, and crab megalope) and soft-body prey (e.g., polychaetes, clam siphons, chironomid larvae, and nematodes). These results are consistent with previous analyses of the food habits of juvenile winter flounder across their broader geographic distribution (from Newfoundland to Maryland: Stehlik and Meise, 2000, and references therein; Vivian et al., 2000; Shaheen et al., 2001; Link et al., 2002; Meng et al., 2008). Summer flounder also consumed a diverse range of crustaceans (e.g., shrimps, amphipods, copepods, cumaceans, and ostracods) and soft-tissue prey (e.g., polychaetes and clam siphons), as well as 8 identifiable fish species. To the knowledge of the authors, this is the first description of the feeding habits of juvenile summer flounder from southern New England nurseries and, more specifically, from oligomesohaline tidal rivers (mean salinity <20).

The diet of summer flounder described herein corroborate observations from the Middle and South Atlantic Bight (Packer et al., 1999); although geographic differences in conspecific diets are also apparent and are likely due to large-scale spatial variations in prey assemblages. For example, in the Chesapeake Bay, Virginia, mysid shrimp (*Neomysis* spp.), sand shrimp, mantis shrimp (*Squilla empusa*), and fish (bay anchovy [*Anchoa mitchilli*] and weakfish [*Cynoscion regalis*]) accounted for ~91%, by weight, of the total diet of summer flounder 125–224 mm TL (Latour et al., 2008). In the York River, a major tributary of the Chesapeake Bay, mysid shrimp (*N. americana*), palaemonid shrimp, and fish were the favored prey of summer flounder 98–192 mm TL (TL converted from standard length [SL]; Able and Fahay, 1998) (Smith et al., 1984). Summer flounder 100–200 mm TL collected from the Pamlico Sound, North Carolina, similarly ate a large volume of mysid shrimp (*%V*=42%; *N. americana*), fish (38%; engraulids and sciaenids), and decapod shrimps (8%; carideans and penaeids) (Powell and Schwartz, 1979). Conversely, in the polyhaline regions of the Newport and North Rivers, North Carolina (mean salinity: 31–32), the dominant prey of summer flounder 25–73 mm TL (TL converted to SL) were spionid polychaetes and invertebrate parts (e.g., clam siphons), which together composed ~90% of the total *IRI* (*%IRI* = *%N* × *%F*; Burke, 1995). Interestingly, the diet composition of equivalent-size southern flounder (*Paralichthys lethostigma*), which occupied the lower salinity portions of Newport and North Rivers (mean salinity <25), was indicative of the diet of summer flounder examined in this study, in that amphipods (*Gammarus* spp.) and mysid shrimp (*N. americana* and *Americamysis bigelowi*) were the most important prey categories for this congener species (combined *%IRI*: ~90%; Burke, 1995).

Intraspecific diet diversity and niche breadth

Despite the evidence that winter flounder and summer flounder are feeding generalists (i.e., according to cumulative prey taxa consumed), this study also revealed that certain prey contributed disproportionately to the diet of each species. Three prey taxa specifically accounted for >85% of the overall diet of both species: amphipods, copepods, and polychaetes (combined *%IRI*: ~88%) for winter flounder and mysid shrimp, sand shrimp, and amphipods (combined *%IRI*: ~ 86%) for summer flounder. The inequitable dietary contributions of these favored prey were reflected in the *B* (values ≤0.4), where low values indicated specialized feeding behavior (Levins, 1968; Novakowski et al., 2008).

Although winter and summer flounder generally are considered opportunistic feeders (Packer et al., 1999; Pereira et al., 1999), there are previous accounts of these species selectively foraging on prey that are in low abundance (Carlson et al., 1997; Shaheen et al., 2001; Latour et al., 2008; Meng et al., 2008). It is important to reiterate, however, that food niche breadth of winter and summer flounder was predator-size dependent, such that a moderate to high degree of diet diversity was observed in larger juveniles (>75 and 115 mm TL, respectively). The broadening of dietary breadth with increasing lengths of winter and summer flounder is attributed to the concomitant enlargement of mouth gape and improved prey detection and capture abilities in larger fish (Mulkana, 1966; Manderson et al., 2000; Stehlik and Meise, 2000; Vivian et al., 2000). Further, as observed in winter flounder, spatially explicit variations in niche breadth may be a reflection of site-specific patterns in prey diversity and availability (Mulkana, 1966; Rudnick et al., 1985); for example, winter flounder have a greater niche breadth in the Taunton River because this system possibly maintains a higher abundance of novel prey.

Ontogenetic and spatiotemporal effects on intraspecific diets

Direct visual analysis of the stomach contents of winter flounder and summer flounder affirmed ontogenetic shifts in their respective diets. Winter flounder <40 mm TL predominantly fed on harpacticoid and calanoid copepods, transitioning to amphipods, isopods, and bivalves with increasing size. The principal prey of summer flounder <60 mm TL were mysid shrimp and copepods, whereas sand shrimp, amphipods, and fish were the dominant prey of larger conspecifics. Similar size-dependent effects on feeding habits of winter and summer flounder have been reported throughout the broader geographic distribution of each species. In the Navesink River and Sandy Hook Bay, New Jersey, for example, small winter flounder (<50 mm TL) fed mainly on copepods (calanoids and harpacticoids), small polychaetes (e.g., spionids), and amphipods (e.g., ampeliscids) (Stehlik and Meise, 2000). Subsequent increases in size (50–90 mm TL) of winter flounder resulted in a greater reliance on amphipods and a dietary switch toward larger polychaetes (e.g., nereidids), mollusks (softshell [*Mya arenaria*] and *Nassarius* spp.), and other crustaceans (mysid shrimp, sand shrimp, and isopods) (Stehlik and Meise, 2000). Comparable size-dependent patterns in feeding behavior of winter flounder were documented also in the Hudson River estuary, New York (20–65 mm TL; Vivian et al., 2000), Pettaquamscutt River, Rhode Island (10–80 mm TL; Mulkana, 1966), and Massachusetts coastal waters (<25–100 mm TL; Linton, 1921).

The diet of metamorphic summer flounder (10.4–18.2 mm TL, converted from SL) from the Great Bay–Little Egg Harbor estuary, New Jersey, was dominated by the calanoid copepod *Temora longicornis* (*%IRI*=86.2%), indicating a pelagic feeding strategy (Grover, 1998). Recently settled summer flounder also forage on calanoid and harpacticoid copepods in North Carolina coastal embayments (11.5–24.7 mm TL, converted from SL; Burke, 1995) and Georgia tidal creeks (11.5–48.6 mm TL, converted from SL; Reichert and van der Veer, 1991), but the use of this prey resource

diminished rapidly as the body size of summer flounder increased. Numerous studies have also reported the significance of mysid shrimp in the diet of juvenile summer flounder throughout the geographic range of this species (from New York to Georgia: Kimmel, 1973; Smith and Daiber, 1977; Festa[5]; Powell and Schwartz, 1979; Lascara, 1981; Wenner et al.[6]; Reichert and van der Veer, 1991; Burke, 1995; Timmons, 1995; Manderson et al., 2000; Link et al., 2002; Latour et al., 2008; Buchheister and Latour, 2011; Sagarese et al., 2011). However, the dietary contributions of mysid shrimp typically declined with the increasing size of summer flounder, and this prey resource was replaced by other macrocrustaceans (sand shrimp, mantis shrimp, and crabs), fish, and squid (Powell and Schwartz, 1979; Link et al., 2002; Latour et al., 2008; Buchheister and Latour, 2011).

Significant spatiotemporal variability was observed in the diet composition of winter and summer flounder in this study. These observed patterns may be partly attributed to differences in the size structure of winter and summer flounder across riverine sites and to progressive increases in body size over time (Taylor et al., 2016)—the latter resulting in ontogenetic dietary shifts, as described above. Alternatively, the observed food habits of winter and summer flounder may reflect habitat and seasonal variations in prey composition (Rudnick et al., 1985; Meng et al., 2008), which have previously been reported to affect the diet of both species (Mulkana, 1966; Burke, 1995; Manderson et al., 2000; Stehlik and Meise, 2000; Latour et al., 2008). Spatiotemporal variations in prey assemblages were not assessed in this study; however, prior investigations in the Narragansett Bay have revealed substantial changes in abundances of benthic meiofauna and macrofauna across sites and seasons (Rudnick et al., 1985; Calabretta and Oviatt, 2008), and some of these fauna constitute important prey for juvenile winter and summer flounder (e.g., harpacticoid copepods, polychaetes, nematodes, and bivalves).

Interspecific dietary overlap

The feeding habits of winter flounder and summer flounder differed significantly from each other, but the extent of dietary overlap was affected by their respective body sizes. According to assessments with the Schoener index, there was minimal dietary overlap of flounder species when comparisons were made independent of body size ($\alpha<0.4$; Hartman and Brandt, 1995; Novakowski et al., 2008; Zahn Seegert et al., 2014)—a finding that indicated food niche segregation. For winter and summer flounder of equivalent sizes, however, dietary overlap was inversely related to total length. Moderate to high resource overlap occurred among small winter and summer flounder (<40 mm TL) and was attributed to their mutual reliance on copepods and, to a lesser extent, amphipods. Ontogenetic dietary shifts exhibited by winter and summer flounder then resulted in notable deviations in their food habits, although amphipods remained a common prey among larger individuals (up to 85 mm TL).

Multiple species of flatfish often coexist in nursery habitats as juveniles (Burke, 1995; Rooper et al., 2006; Nissling et al., 2007; Mariani et al., 2011), leading to potential interspecific competition (Złoch and Sapota, 2010). Niche overlap is typically minimized, however, because of differences in prey preferences (i.e., biological or diet segregation) or fine-scale distribution patterns within the nursery (i.e., physical or spatiotemporal segregation), the latter in response to heterogeneous environmental conditions (Burke, 1995; Rooper et al., 2006; Mariani et al., 2011). Moreover, occurrences of significant dietary overlap of flatfish species do not necessarily result in competitive interactions, given that the foraging rates of most juvenile flatfish are insufficient to reduce prey abundances to levels that are biologically limiting (Kuipers, 1977; Evans, 1983; Shaw and Jenkins, 1992).

In this study, resource partitioning did not occur through spatiotemporal segregation, considering that ~84% of the seine hauls that collected summer flounder also yielded winter flounder. Alternatively, the relatively low degree of dietary overlap of flounder species was attributed to interspecific differences in prey preferences, and dietary differences were most evident at larger body sizes of winter and summer flounder. The diet segregation between winter and summer flounder may also be explained by differences in their respective feeding morphologies. Summer flounder have a relatively large mouth with canine-like teeth (Woolcott et al., 1968), which enables the capturing and processing of larger prey items (Manderson et al., 2000). In contrast, the small mouth and reduced gape size of winter flounder imposes morphological constraints on their diet, which is limited to small-body prey throughout their development (Stehlik and Meise, 2000; Vivian et al., 2000).

This study does provide some evidence of significant dietary overlap for small winter and summer flounder (<40 mm TL); yet it is hypothesized that the abundances of either flounder species did not attain levels where interference or exploitative competition could cause the limitation of food resources (Evans, 1983; Modin and Pihl, 1994; Iles and Beverton, 2000; Taylor et al., 2016). Accordingly, the failed recovery of winter flounder in southern New England habitats, including the Narragansett Bay and contiguous waters (Collie et al., 2008; NEFSC[2]), does not appear to be associated with putative competition with juvenile summer flounder.

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Patterns of courtship acoustics and geophysical features at spawning sites of black grouper (*Mycteroperca bonaci*)

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Abstract—Geomorphological assessments were conducted and passive acoustic recordings were collected from 2012 through 2014 at 3 recently identified spawning aggregations of the black grouper (*Mycteroperca bonaci*) in Puerto Rico and southern Florida. A time series of courtship-associated sounds (CASs) by black grouper were analyzed in relation to lunar and diel periodicities, water temperature, and tidal stage. Analysis of CAS recordings indicated similar temporal patterns at the 3 spawning aggregations. Spawning season was correlated with decreased water temperature. Within the spawning season, CAS production was influenced significantly by lunar and diel periodicities and sound production peaked between the last quarter and new moons during evening hours. The data from this study also indicate a potential correlation with tidal stage. Temporal patterns were similar during 3 consecutive years at Mona Island in Puerto Rico and for the geographically isolated sites of Mona Island and Riley's Hump off Florida. At Bajo de Sico in Puerto Rico, courtship activity was lower than that at the other sites but reflected the same general patterns in 2014. For all 3 sites, spawning aggregations were found less than 150 m from a promontory at depths between 25 and 35 m near deep water (>100 m).

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Most large, western Atlantic groupers (family Epinephelidae) form site-specific transient fish spawning aggregations (FSAs) at predictable times throughout the year (Domeier and Colin, 1997). Large proportions of the annual catch of species that form transient FSAs occur when these fish are aggregated (Claydon, 2004). Consequently, groupers are vulnerable to intense fishery pressure (Eklund et al., 2000; Brulé et al., 2003). Combined with the protogynous hermaphroditism, slow growth, and late maturation common to large groupers, many species of grouper are experiencing population declines due to the removal of spawning stocks at aggregations (Matos-Caraballo, 1997).

The black grouper (*Mycteroperca bonaci*) is the second largest grouper in the western Atlantic and is classified as near threatened in the IUCN Red List of Threatened Species because of declining populations (Ferreira et al., 2008). Although black grouper can spawn year-round (Crabtree and Bullock, 1998), the majority of their annual reproductive effort is spent seasonally during transient spawning aggregations (García-Cagide and García, 1996; Crabtree and Bullock, 1998). Only 3 spawning aggregations of black grouper have been described within U.S. territorial waters (Eklund et al., 2000; Schärer et al., 2014; Locascio and Burton, 2016). However, black grouper are believed to form many small spawning aggregations throughout their range (Paz and Sedberry, 2008).

Identification, characterization, and assessment of FSAs are critical for effective management of populations (Claydon, 2004). Geomorphological assessments of 5 multispecies FSA sites used by large groupers (with 1 site documented for black grouper) revealed consistent benthic morphometric parameters across sites (Kobara and Heyman, 2008). Furthermore, follow-up analyses of bathymetry maps at 12 known FSA sites in Belize (10 supporting black grouper) led to the documentation of 2 additional multispecies aggregations, both of which included black grouper (Kobara and Heyman, 2010).

Black grouper form spawning aggregations at different times of the

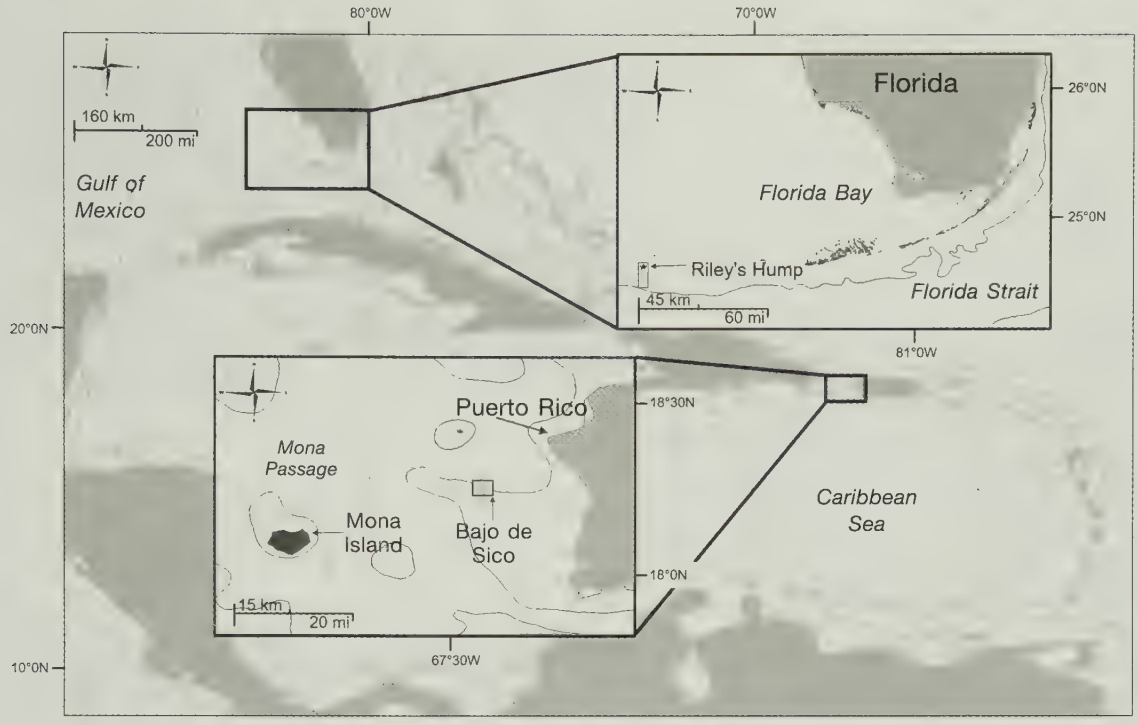

Figure 1

Map of the 3 study sites sampled in this study of acoustic courtship of black grouper (*Mycteroperca bonaci*) in Puerto Rico and off southern Florida during 2012–2014. Top right excerpt shows the location of Riley's Hump within the Tortugas South Ecological Reserve off southern Florida. Bottom left excerpt shows locations of the Bajo de Sico seasonal no-take reserve and Mona Island off Puerto Rico. Contour lines indicate 200- and 2000-fathom bathymetry.

year throughout their range in water temperatures of 25–28°C from the east coast of Brazil, through the Caribbean and Gulf of Mexico, to Bermuda (Brulé et al., 2003; Teixeira et al., 2004; Paz and Sedberry, 2008; Luckhurst, 2010). At aggregations, increases in the number of black grouper correlate with the period between the full moon and new moon and during dusk hours, when the only direct observations of gamete release have been made (Sala et al., 2001; Paz and Sedberry, 2008). Although general temporal patterns are known, the specifics of spawning timing are not, and it is believed that site-specific temporal patterns of spawning are likely to respond to local environmental variations. Passive acoustic monitoring of FSAs of red hind (*Epinephelus guttatus*) off western Puerto Rico, for example, has shown that peak courtship sound production occurs at different times (Mann et al., 2010; Appeldoorn et al., in press) even between sites located within 12 km of each other on the same shelf. This observation indicates that the dynamics of FSAs are variable locally—a finding that has implications for best management practices and local conservation measures (e.g., closed seasons).

Courtship sounds are common throughout the epinephelids (Mann et al., 2009, 2010; Nelson et al., 2011, Schärer et al., 2012a, 2012b), and male black grouper are no exception, producing a species-specific courtship sound associated with spawning behavior (Schärer et al., 2014; Locascio and Burton, 2016). With passive acoustic monitoring, therefore, it is possible to conduct a more detailed analysis of the courtship patterns of black grouper than current methods allow (Rowell et al., 2011, 2015). Traditionally, FSAs are monitored by using diver surveys and analysis of gonadal-somatic indices (GSIs). However, passive acoustic monitoring has 3 advantages: 1) field work is not subject to marine conditions or physiological limitations; 2) data collection is long term and occurs on a set recording schedule; and 3) multiple sites can be monitored simultaneously (Gannon, 2008; Luczkovich et al., 2008).

Reproductive behavior needs to be understood thoroughly to develop and implement effective management policy. The objectives for this study were 1) to use high-resolution acoustic time series to study the interannual variability of temporal patterns at a spawning aggregation of black grouper and intra-annual variability between 2 geographically separate FSAs, 2) to conduct an initial assessment of an undocumented spawning aggregation of black grouper, and 3) to characterize the morphometric parameters of the 3 sites where black grouper aggregate and test whether their geophysical features are consistent with predictions derived from previously described sites.

Materials and methods

Study sites

Mona Island is a carbonate platform located approximately 73 km west of Cabo Rojo, Puerto Rico (Fig. 1). The Mona and Monito Islands National Reserve extends from the coast out to 17 km (9 nautical miles); a year-round no-take zone encompasses all waters around the island within 13 km (7 nautical miles) of shore. The island itself is a flat-topped, raised platform with continuous vertical cliffs around almost the entire perimeter. Along the south–southwestern insular shelf, there is a shallow lagoon bordered by coral reefs along the seaward end (Frank et al., 1998). The spawning aggregation of black grouper at this site is located along the southern shelf edge bordered by a steep reef wall. Courtship interactions, ventral rubbing, and courtship colorations of black grouper were previously recorded at this site in conjunction with courtship-associated sound (CAS) production (Schärer et al., 2014).

Riley's Hump is a small carbonate reef bank to the southwest of the Dry Tortugas within the Tortugas South Ecological Reserve, Florida—a fully protected marine reserve (Fig. 1). This reef bank is a multispecies FSA site and a year-round no-take zone. The bank crest rises to a 30-m depth at its shallowest point, and the southern and western edges of the platform are composed of a steep reef wall (Weaver et al., 2006). This spawning aggregation of black grouper at this site is located on a pinnacle off the southwestern corner of the crest of the seamount. In previous years, courtship interactions of black grouper were documented in combination with recorded CASs along the southern wall (Locascio and Burton, 2016).

Bajo de Sico is a seamount located approximately 27 km west of Mayagüez, Puerto Rico (Fig. 1). A seasonal marine protected area, it is closed to fishing from 1 October to 31 March for all reef fish species regulated by the Caribbean Fishery Management Council. Consisting of 31.2 km^2, this seamount is jointly managed by Puerto Rico and U.S. federal jurisdictions. This seamount supports hermatypic corals at depths between 40 and 90 m and has vertical drop-offs along its western and northwestern edges. Courtship behavior of black grouper was witnessed (senior author, personal observ.) in an area characterized by a steep reef wall and large rock promontory.

Passive acoustic recording

Digital spectrogram recorders (DSG-Ocean[1], Loggerhead Instruments, Sarasota, FL) were deployed at all 3 sites preceding aggregation of fish (Table 1). One digital spectrogram (DSG) recorder was deployed at the known FSA location at Mona Island. Multiple DSG recorders were deployed around the spawning areas at Riley's Hump and Bajo de Sico. For each of those 2 sites, data from the DSG recorder with the most CAS recordings were used for analysis. High CAS rates, high sound levels, and temporal patterns of CASs from each selected DSG recorder indicate a strong likelihood of close proximity to a spawning location.

Table 1

Dates of deployment and recovery of autonomous acoustic digital spectrogram recorders used for analysis of production of courtship-associated sounds made by black grouper (*Mycteroperca bonaci*) at 2 sites in Puerto Rico (Mona Island and Bajo de Sico) and 1 site off southern Florida (Riley's Hump) during 2012–2014. Deployment and recovery specifically refer to beginning and end dates of time-series data used in analysis.

Year	Site	Deployment	Recovery
2012	Mona Island	12/20/11	4/30/12
	Riley's Hump	12/18/11	5/29/12
2013	Mona Island	12/20/12	4/30/13
	Bajo de Sico	12/16/12	4/30/13
2014	Mona Island	12/28/13	4/30/14
	Bajo de Sico	12/20/13	4/30/14

The DSG recorders at Bajo de Sico and Mona Island collected 20-s audio clips every 5 min during deployment (Table 1). At Riley's Hump, the DSG recorder collected 10-s audio clips every 10 min during deployment (Table 1). Differences in these recording schedules required different corrective factors to extrapolate total CASs from sample size to daily totals for comparison. Daily total recorded CASs at Riley's Hump were multiplied by 60 to calculate the total number of CASs per day. Daily total recorded CASs at Bajo de Sico and Mona Island were multiplied by 15 to calculate total number of CASs per day. After recovery of DSG recorders, recorded files were downloaded and converted to .wav format for visual analysis with Ishmael software, vers. 2.4 (Cooperative Institute for Marine Resources Studies Bioacoustics Lab, Oregon State University, Newport, OR) (Fig. 2). Any questionable CASs were verified audibly by using Windows Media Player and noise cancelling headphones. Audible detection of a pulse train undulation that was specific to black grouper at a frequency band between 75 and 100 Hz served as species verification.

Temporal analysis

The total number of CASs per day from each DSG recorder was calculated for each calendar day during deployment. The monthly averages of daily total numbers of CASs were compared to confirm seasonality. Daily total numbers of CASs were analyzed in relation to the number of days after a full moon (DAFM) to analyze patterns associated with lunar periodicity.

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

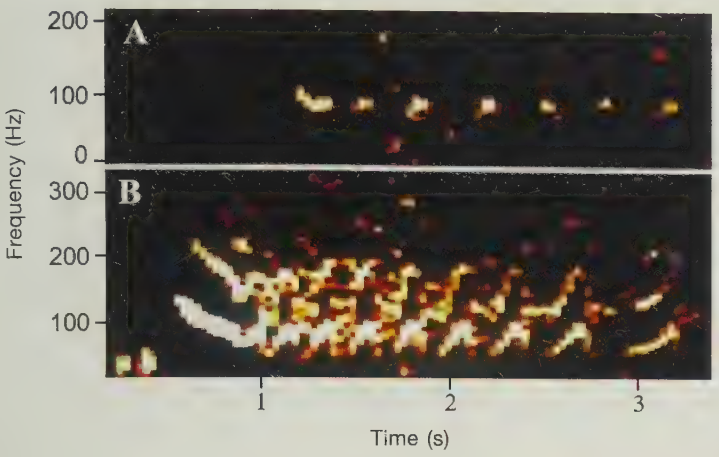

Figure 2

Examples of (**A**) strong and (**B**) weak spectrograms of courtship-associated sounds (CASs) made by black grouper (*Mycteroperca bonaci*) and collected by a digital spectrogram recorder at Bajo de Sico, Puerto Rico, in 2013. Presence of pulse train undulation specific to black grouper within the frequency band of 75–100 Hz is visually detectable in both spectrograms. The *x*-axis is time in seconds. The *y*-axis is frequency in hertz. Brightness of yellow color indicates increased strength of CAS call.

The calendar day with a rising full moon (local time) was considered day 0. Each successive day was considered another DAFM, until the next day of a rising full moon. Daily total numbers of CASs during periods of increased courtship calling were broken down into hour blocks. Hourly totals during these periods of increased activity were summed over the entire analysis period to examine daily patterns.

For each site, analysis of variation was done with Fisher's least significant difference test to determine differences between daily numbers of CASs for DAFM and hourly numbers of CASs for periods of increased activity.

Temperature

Temperature loggers (HOBO Water Temp Pro v2, Onset Computer Corp., Bourne, MA) were deployed at Mona Island and Bajo de Sico from 3 January to 31 April 2014. Temperature data from Mona Island was recorded at a spawning aggregation of red hind, nearby the spawning aggregation of black grouper, at a depth of 30 m. Temperature data from Bajo de Sico was recorded at the site of a DSG recorder, nearby the spawning aggregation of black grouper, at a depth of 45 m.

Site geophysical features

Geophysical features of the sites were analyzed by using the methods from Kobara and Heyman (2008). Analysis was done in ArcGIS 10.3 (Esri, Redlands, CA) with the Spatial Analyst and 3D toolboxes. For the morphometric analysis, the specific location of each DSG recorder that supplied data used in acoustics analysis was considered the location of the FSA. That point location was overlaid on high-resolution multibeam bathymetry maps for Bajo de Sico and Mona Island (Battista[2]). A 1-km-radius buffer around the location of the recorder was isolated from the bathymetry map. Depth was converted to slope and slope was extracted into contours. Slope contours were superimposed on depth. The "shelf edge" was classified as the continuous 20°-slope contour at a steep vertical depth profile off the shallower structure. The structure outlined within the 1-km buffer area was used to visually identify promontories along the shelf edge. A promontory was defined as a noticeable convex protrusion extending off the contour of the shelf edge within the 1-km-radius scale.

The morphometric parameters measured were the shortest distances from the FSA to 1) the shelf edge, 2) the 30-m depth contour, and 3) the horizontal inflection point defining the nearest promontory feature. The depth of the shelf edge was measured at its nearest point to the FSA location. The aggregation of black grouper at Riley's Hump was not analyzed through bathymetric data; but the above parameters were read from an existing bathymetric map from Locascio and Burton (2016), originally published in Mallinson et al. (2003).

Results

Temporal analysis

Mona Island Mean daily CAS rates peaked in February for all 3 years, from 2012 through 2014, at Mona Island. Production of CASs increased between the last quarter moon and the new moon, from 8 to 14 DAFM (Table 2). Production of CASs increased between 8 and 12 DAFM (Fig. 3). CASs were correlated strongly with time of day (Table 3). During the 3 seasons at Mona Island, 54% of all recorded CASs by black grouper occurred during a 2-h period between 1700 and 1900 h local time (Fig. 4). The 4-h period between 1600 and 2000 h, 16% of the day, contained 68% of the total number of CASs produced (Fig. 4).

[2] Battista, T. 2015. Water depth and acoustic backscatter data collected from NOAA Ship *Nancy Foster* in Caribbean Sea, southern coast of Isla de Mona, western coast of Puerto Rico from 2007-04-14 to 2007-04-24 (NCEI Accession 0131853). Version 1.1. NOAA National Centers for Environmental Information, Silver Spring, MD. [Data set available from website.]

Table 2

Results of analysis of variance tests comparing the dependent variable mean number of courtship-associated sounds per day against the independent variable days after full moon for this study of acoustic courtship of black grouper (*Mycteroperca bonaci*) during 2012–2014 at Riley's Hump (RH) off southern Florida and at Mona Island (MI) and Bajo de Sico (BDS). *N*=total number of days recorded. df=degrees freedom. MS=means squared.

Site and year	*N*	df	MS	*F*	*P*-value
RH 2012	149	29	5.43	3.89	<0.0001
MI 2012	120	29	12.43	4.38	<0.0001
MI 2013	119	29	21.59	3.98	<0.0001
MI 2014	120	29	22.33	3.93	<0.0001
BDS 2013	119	29	4.74	2.06	<0.0001
BDS 2014	120	29	7.47	1.81	0.0178

Table 3

Results of analysis of variance tests comparing the dependent variable mean hourly numbers of courtship-associated sounds against the independent variable hour of day for this study of acoustic courtship of black grouper (*Mycteroperca bonaci*) during 2012–2014 at Riley's Hump (RH) off southern Florida and at Mona Island (MI) and Bajo de Sico (BDS). *N*=hours of day (24)×number of months analyzed. df=degrees freedom. MS=mean square.

Site and year	*N*	df	MS	*F*	*P*-value
RH 2012	144	23	6.78	6.99	<0.0001
MI 2012	120	23	37.84	19.83	<0.0001
MI 2013	120	23	79.59	31.79	<0.0001
MI 2014	120	23	80.93	13.77	<0.0001
BDS 2013	120	23	2.78	2.34	0.0034
BDS 2014	120	23	9.21	4.68	<0.0001

Riley's Hump The daily mean number of CASs peaked in April at Riley's Hump in 2012, increasing 2-fold from the month of lowest activity, February. Production of CASs increased from 7 to 11 DAFM, and peaked at 10 DAFM (Fig. 3). Daily production of CASs was correlated strongly with time of day (Table 3). Of all CASs at Riley's Hump, 35% occurred in a 2-h window from 1600 to 1800 h local time. Almost half (48%) of all CASs occurred from 1500 to 1900 h local time (Fig. 4).

Bajo de Sico At Bajo de Sico, CAS counts were substantially lower than counts recorded at Mona Island and Riley's Hump. Daily mean number of CASs peaked in January. Production of CASs increased from 4 to 10 DAFM (Fig. 3) in 2013; however, no defined peak period was evident. In 2014, peaks were more defined. Production of CASs increased 6–9 DAFM (Fig. 3). Similar variation in hourly numbers of CASs was found between the 2 years at Bajo de Sico. Hour was determined to be significant (Table 3) for both years; however, patterns were more evident in 2014 (Fig. 4).

Temperature

Temperature time-series data for 2014 indicated decreasing temperatures from January to March (Fig. 5). In March, temperatures remained near annual minimums before beginning to increase in April. At both Bajo de Sico and Mona Island, temperatures dropped below 27°C from mid-January to mid-April. Temperatures remained slightly lower at Bajo de Sico than at Mona Island but only by tenths of a degree Celsius, potentially a result of deployment of the temperature logger at a depth of 45 m at Bajo de Sico compared with deployment at a depth of 30 m at Mona Island.

Site geophysical features

All 3 spawning sites fell within the geophysical parameters described for multispecies FSAs in the Cayman Islands and Belize (Table 4). The Bajo de Sico and Mona Island spawning sites were less than 100 m from convex promontories, less than 100 m from the shelf edge, and in an area where the shelf edge is found at depths of 25–30 m. Similar geophysical parameters were evident at Riley's Hump. This site was situated at a depth of approximately 35 m and was adjacent to deep water (>100 m). All 3 sites were within 500 m of a 30-m vertical wall.

Discussion

The 3 spawning aggregations of black grouper had comparable patterns in their CAS production (Figs. 3 and 4) and site geophysical features (Table 4). Selected sites exhibited definable geophysical parameters that can be used to identify undocumented FSAs. In addition, distinct, well-defined, comparable patterns in CAS production were observed at 2 of the 3 FSAs analyzed in this study. Patterns of sound production at Mona Island were very similar over the 3 years. Seasonal timing of CAS production at Mona Island had little interannual variability, when examined in relation to DAFM and time of day, and was similar to temporal patterns observed at Riley's Hump. Elevated periods of CASs production at Riley's Hump were observed monthly during December–April, except January.

At Bajo de Sico, CAS temporal patterns varied between the 2 seasons during which passive acoustic recordings were collected. In 2013, there were periods of

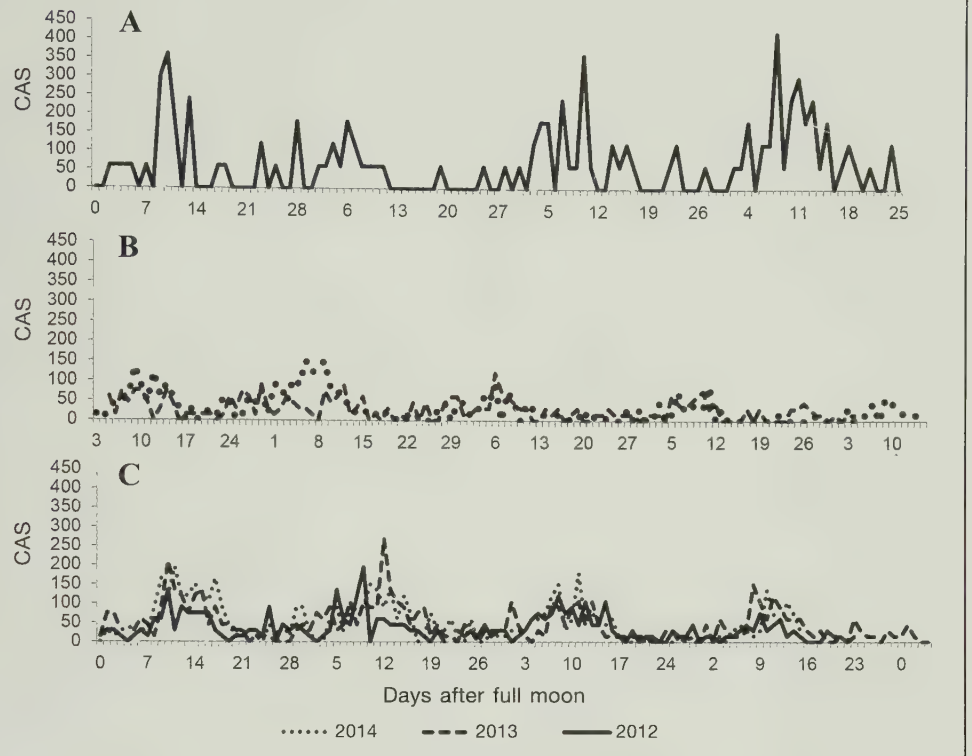

Figure 3

Total number of courtship-associated sounds (CASs) made by black grouper (*Mycteroperca bonaci*) per day for the corresponding day after a full moon (DAFM) at 3 spawning aggregations of black grouper: (**A**) Riley's Hump off southern Florida and, in Puerto Rico, (**B**) Bajo de Sico and (**C**) Mona Island. This time series begins at first full moon of each spawning season, from mid-December to mid-January. Quantities of CASs are extrapolated out from sampling schedule to whole day. *Y*-axes are expanded to magnify temporal patterns.

elevated CAS rates in January–April, but intraseasonal variability was low and lacked any definable patterns. In 2014, the CAS patterns at Bajo de Sico were similar to those observed at Mona Island and Riley's Hump. The production of CASs increased significantly on days approaching the last quarter and new moons during late afternoon hours. This shift indicates a change in the use of the study site by black grouper at Bajo de Sico, as CAS production here is considered an indirect measure for reproductive activity. Either the location was a spawning site during both seasons and the temporal dynamics changed between years, or, more probably but equally intriguing, Bajo de Sico was used only as a spawning location in 2014. This question needs to be addressed to better understand the local variations of temporal patterns at Bajo de Sico.

The monthly mean number of CASs per day coincided with the months of lowest annual temperature during 2014 at Mona Island and Bajo de Sico. In January, February, and March, average temperatures at these 2 sites were below 27°C before beginning a warming trend in late March. April was the first month with average temperatures above 27°C. Additionally, at Mona Island, the minimum temperature for 2014 occurred during February, the month with the highest CAS activity for all 3 years. Black grouper spawn in the temperature range of 25–28°C throughout their distribution. Within the greater Caribbean and Gulf of Mexico regions, FSAs form in winter months (García-Cagide and García, 1996; Eklund et al., 2000; Brulé et al., 2003; Paz and Sedberry, 2008; Schärer et al., 2014) when temperatures decrease to their annual minimums. In Bermuda, they occur during summer when sea-surface temperatures increase to 26–28°C (Luckhurst, 2010), and, in Brazil, the GSI index was highest during the winter months of August and September (Teixeira et al., 2004) when average temperatures cooled to 27°C (World Sea Temperatures, website). These temperature ranges have increased egg hatching success and larval survival of leopard grouper (*Mycteroperca rosacea*), Malabar grouper (*Epinephelus malabaricus*), and Nassau grouper (*Epinephelus striatus*) in controlled laboratory experiments (Watanabe et al., 1995; Gracia-López et al., 2004; Yoseda et al., 2006) and indicate that ocean

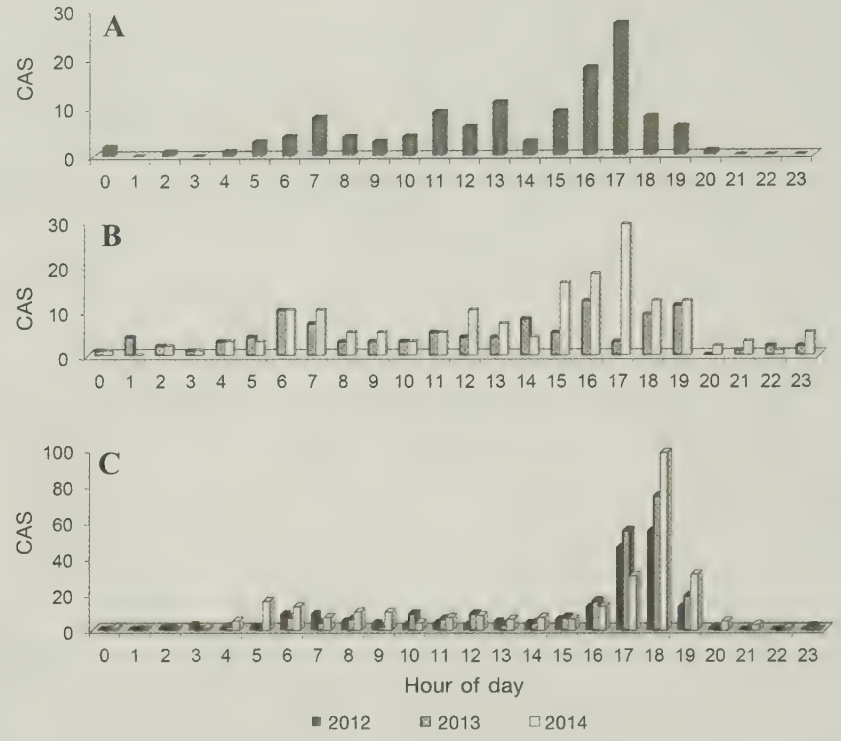

Figure 4

Total numbers of courtship-associated sounds (CASs) produced by black grouper (*Mycteroperca bonaci*) per hour summed during entire deployment at 3 spawning sites: (**A**) Riley's Hump off southern Florida and, in Puerto Rico, (**B**) Bajo de Sico and (**C**) Mona Island. Hourly totals are summed from days of increased spawning activity. All times are in local Atlantic Standard Time (–4GMT).

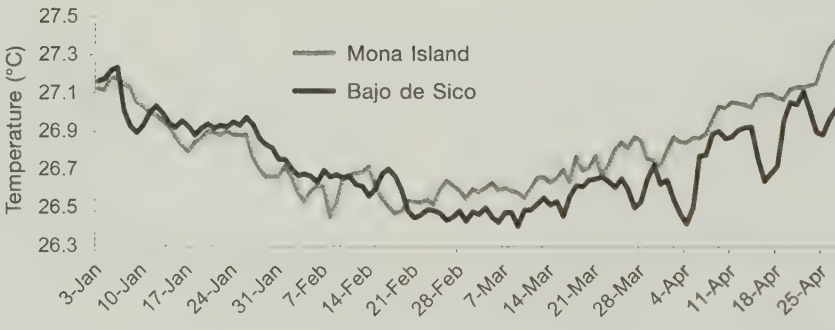

Figure 5

Time series of temperatures at Mona Island (30-m depth) and Bajo de Sico (45-m depth) in Puerto Rico from 3 January to 30 April 2014.

temperatures are a seasonal controlling factor for the formation of spawning aggregations of black grouper.

The CAS rate increased significantly between the last quarter moon and the new moon at all 3 sites (Fig. 3). Between the last quarter and new moon, moonrise occurs after sunset. Furthermore, during these lunar stages, CAS production peaked during late afternoon hours (Fig. 4). More than half of all CASs produced over the 3 years at Mona Island occurred within a 2-h period around sunset. At Riley's Hump, almost half

Table 4

Geophysical parameters of spawning aggregations of black grouper at Mona Island (MI) and Bajo de Sico (BDS) in Puerto Rico. Deployment location of digital spectrogram recorders served as proxy for spawning aggregation site. An asterisk (*) indicates that the expected mean and standard deviation (SD) were calculated from sites that included a spawning aggregation of black grouper (*Mycteroperca bonaci*) seen in Table 1 in Kobara and Heyman (2010).

	Promontory shape	Promontory orientation	Shelf edge depth (m)	Distance to shelf edge (m)	Distance to inflection point (m)	Distance to 100-m depth (m)
MI	Convex	South	27	10	24	63
BDS	Convex	West	28	19	94	233
Mean*			36	25	127	59
SD*			10	25	94	35

(40%) of CASs were produced 1 h before sunset. It seems likely that courtship behavior, and presumably spawning, occurred mainly during the approaching low-light afternoons with no rising moon. This timing is shared by most large groupers in the western Atlantic (Colin at al., 1987; Sala et al., 2001; Schärer et al., 2012b; Locascio and Burton, 2016). Evolution of dusk spawning has been suggested to control predation on both spawning adults and larvae for species that form transient spawning aggregations (Johannes, 1978; Colin and Clavijo, 1988). Evening spawning could provide an approximate 12-h period of darkness for dispersal of eggs away from the aggregation site.

Tidal stage is directly related to moonrise. Beginning 9 DAFM, sunset coincides with the outgoing tide at Mona Island (NOAA Tides and Currents, website), increasing the likelihood that eggs are transported off the reef and away from egg predators (Johannes, 1978). Along the western insular shelf of Puerto Rico, tidal currents are thought to play an important role in spawning timing for the red hind (Appeldoorn et al., in press), and tides have been shown to correlate with spawning timing in other locations (Johannes, 1978; Heppell et al, 2008). Although the effects of light and current are confounded within a single site, they are not confounded across sites. Unlike the conditions at Mona Island and Bajo de Sico, CAS peaks at Riley's Hump did not coincide precisely with sunset hours but occurred slightly earlier. However, the exact time of spawning and the patterns of current flow at Riley's Hump are not known, and current flows can be widely variable because of variations in the location of the Florida current. The significance of this offset and the relative effects of light and currents as factors controlling spawning need further study.

At Mona Island, black grouper aggregate around a specific geological feature. Whether this site is the actual location of spawning or a part of a larger courtship arena (Nemeth, 2012) is unknown. Dive surveys were not conducted in this study during early evening hours, the time at which spawning has been observed in Belize (Sala et al., 2001; Paz and Sedberry, 2008). However, the significant increases in CAS rates during the hours of dusk indicate that spawning was occurring, at least, nearby. This CAS pattern indicates that the aggregation forms within close proximity of the location of the DSG recorder—a conclusion that coincides with the morphometric analysis of nearby geological features (Table 4).

The DSG recorder at Mona Island was deployed 10 m from the shelf edge and sat at a depth of 30 m. Off the shelf edge, there is a step feature, where the bottom briefly levels out at 40 m before a second steep slope. Within 25 m of the DSG recorder is a promontory along the shelf edge. All features are consistent with morphometric parameters of multispecies spawning aggregations in the Cayman Islands and Belize (Kobara and Heyman, 2008; 2010). These features are also common to Bajo de Sico and indicate similar geophysical characteristics for FSA site selection. Although some variation exists within the geomorphology at spawning aggregations of black grouper (Paz and Sedberry 2008; Luckhurst, 2010), similar morphometric parameters have been observed for many documented FSAs, and these parameters can be used to potentially identify new FSAs (Kobara and Heyman, 2010).

Transient FSAs provide an opportunity to survey the density and health of fish stocks for what are normally considered solitary species (Gannon, 2008; Luczkovitch et al., 2008). Including those in our study, only 4 spawning aggregations of black grouper have been identified in U.S. territorial waters; the largest one is composed of only a couple hundred individuals (Eklund et al, 2000; Schärer et al., 2014; Locascio and Burton, 2016). However, population numbers indicate that black grouper must be spawning at additional sites. Anecdotal evidence of eight additional spawning aggregations of black grouper in Puerto Rico, based on interviews with fisherman, suggests that many other sites must exist, although only

the 1 site at Mona Island has been verified (Ojeda-Serrano et al., 2007).

Strong regularities in temporal patterns in CAS production between 2 geographically separate sites, Mona Island and Riley's Hump, indicate that spawning timing of black grouper is predictable within the greater Caribbean region. Interannual monitoring at Mona Island adds support to these consistencies in temporal patterns. Whether these patterns are population wide will be determined only through further analysis and the incorporation of additional sites within a monitoring program. Identifying new FSAs and developing fine-resolution behavioral models can identify local variations in temporal patterns of spawning behavior and assist in the development of effective management policies.

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First verified occurrence of the shortnose sturgeon (*Acipenser brevirostrum*) in the James River, Virginia

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Abstract—The shortnose sturgeon (*Acipenser brevirostrum*) is an endangered species of fish that inhabits the continental slope of the Atlantic Ocean from New Brunswick, Canada, to Florida. This species has not been documented previously in the freshwater portion of any river of the Chesapeake Bay, except in the Potomac River. On 13 March 2016, a shortnose sturgeon was captured in the freshwater portion of the James River at river kilometer 48. The fish had a fork length of about 75 cm and was likely mature. Genetic analysis confirmed the fish was a shortnose sturgeon and was assigned to the Chesapeake Bay–Delaware population segment. Regardless of whether this shortnose sturgeon was part of a remnant Chesapeake Bay population or whether its capture there is an indicator of an expansion of range from the Delaware River by way of the Chesapeake and Delaware Canal, dedicated research is needed to determine the status of the shortnose sturgeon inhabiting the Chesapeake Bay.

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The shortnose sturgeon (*Acipenser brevirostrum*) is an amphidromous sturgeon reported to inhabit the continental slope of the Atlantic Ocean from New Brunswick, Canada, to Florida (Gruchy and Parker, 1980; Dadswell et al., 1984; Kynard, 1997). However, Dadswell et al. (2013) documented a single shortnose sturgeon captured in a weir in the Minas Basin, an inlet of the Bay of Fundy in Nova Scotia, Canada, and that capture represents a modest extension of the northern range for this species. In the United States, the shortnose sturgeon was listed as endangered in 1967, under the Endangered Species Preservation Act, and is currently protected under the U.S. Endangered Species Act. In 2012, the shortnose sturgeon was listed as a species of concern under the Canadian Species At Risk Act.

The Chesapeake Bay is located roughly in the middle of the reported geographic range of the shortnose sturgeon (Fig. 1), but because of the scarcity of this species, research dedicated to shortnose sturgeon in the Chesapeake Bay has been extremely limited. During 1996–2006, research programs that focused on Atlantic sturgeon (*A. oxyrinchus*) throughout the Chesapeake Bay estuary and that provided a monetary reward for reporting captured sturgeon provided evidence of the capture of shortnose sturgeon, as well (Spells[1]; Welsh et al., 2002; Mangold et al.[2]). Only one genetically verified shortnose sturgeon was collected in Virginia waters as part of these programs (Spells[1]; Welsh et al., 2002). One other fish captured was hypothesized to be a shortnose sturgeon but could not be verified at the species level because no genetic sample was taken (Spells[3]). Both the verified and suspected shortnose sturgeon were collected at the mouth of the Rappahannock River, a marine portion of the Chesapeake Bay estuary. In the Maryland reward pro-

[1] Spells, A. J. 1998. Atlantic sturgeon population evaluation utilizing a fishery dependent reward program in Virginia's major western shore tributaries to the Chesapeake Bay, 5 p. An Atlantic Coastal Fisheries Cooperative Management Act Report for National Marine Fisheries Service. U.S. Fish Wildl. Serv., Charles City, VA. [Available from Harrison Lake National Fish Hatchery, U.S. Fish Wildl. Serv., 11110 Kimages Rd., Charles City, VA 23030-2844.]

[2] Mangold M., S. Eyler, S. Minkkinen, and B. Richardson. 2007. Atlantic sturgeon reward program for Maryland waters of the Chesapeake Bay and tributaries 1996–2006, 22 p. [Summary report] Maryland Fish. Resour. Off., U.S. Fish Wildl. Serv., Annapolis, MD. [Available from website.]

[3] Spells, A. 2014. Personal commun. Harrison Lake National Fish Hatchery, U.S. Fish Wildl. Serv., 11110 Kimages Rd., Charles City, VA 23030-2844.

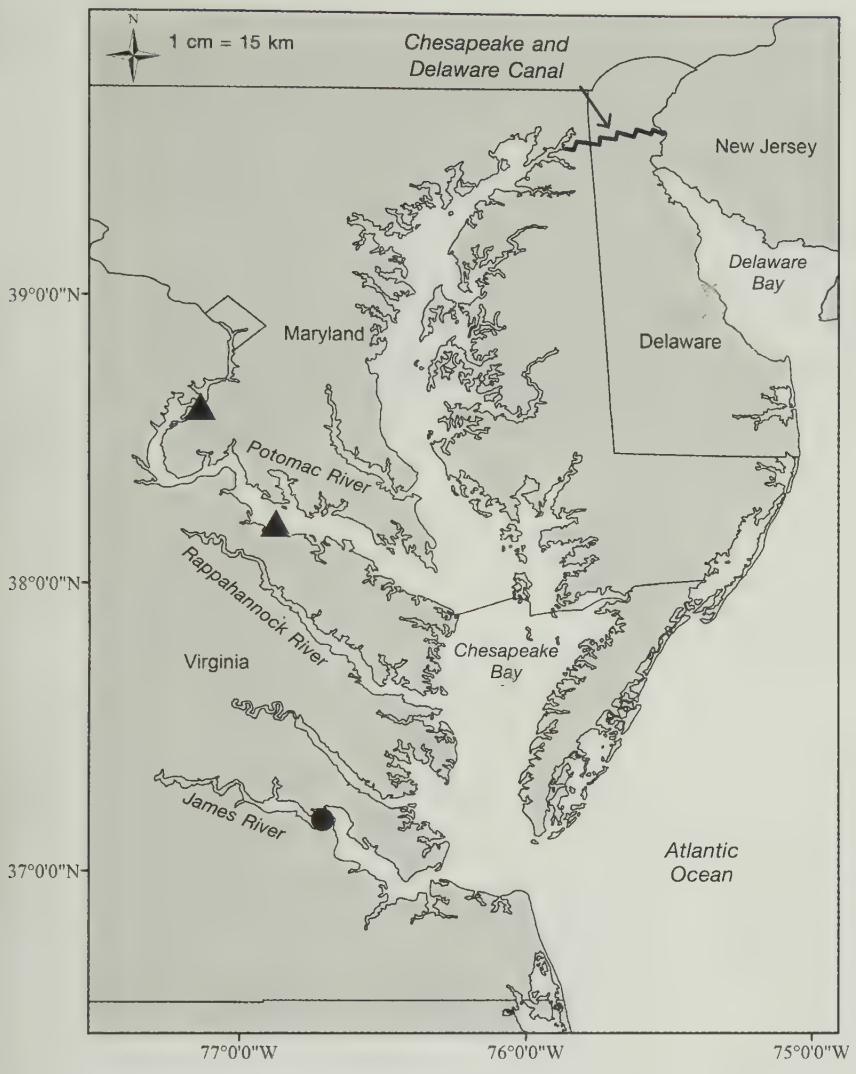

Figure 1

Map of the Chesapeake Bay showing, to our knowledge, all known freshwater locations where shortnose sturgeon (*Acipenser brevirostrum*) were captured in the Chesapeake Bay. The black dot marks the location where the shortnose sturgeon was captured on the James River in this study. The 2 triangles are the capture locations on the Potomac River for the 2 gravid female shortnose sturgeon documented by Kynard et al. (2009).

gram, 72 shortnose sturgeon were documented during 1996–2006; however, because of problems with obtaining collection permits, Maryland scientists were not allowed to tag 26 shortnose sturgeon collected after May of 2002 (Mangold et al.[2]). There is a chance that some of the 26 shortnose sturgeon were unknowingly recaptured during the reward program. Results of analysis of the genetic samples taken from shortnose sturgeon as part of the reward program indicated no distinct difference between fish from the Chesapeake Bay and from the Delaware River and Bay; therefore, the 2 groups were assigned to the same population segment (Grunwald et al., 2002; Wirgin et al., 2010; King et al., 2014). Researchers did not mention milt production or egg release for any of the shortnose sturgeon captured during the programs.

Only 2 studies (Welsh et al., 2002; Kynard et al., 2009) were focused specifically on the life history of shortnose sturgeon in the Chesapeake Bay. Welsh et al. (2002) telemetered 13 shortnose sturgeon, which were initially captured and tagged in the marine part of the estuary. Of these 13 fish, 3 shortnose sturgeon were later detected in the Chesapeake and Delaware Canal or in the Delaware River (Welsh et al., 2002). Kynard et al. (2009) focused their research on the life history of shortnose sturgeon in the Potomac River. After extensive sampling and work with commercial fishermen, they captured 2 shortnose sturgeon. Both fish were gravid females, and telemetric and recapture data indicated that one fish spawned in the Potomac River (Kynard et al., 2009). As with the genetic samples collected during the Chesapeake Bay reward program, the 2 gravid females could not be genetically differentiated from Delaware River shortnose sturgeon (King et al., 2014). As of this writing, the only documented occurrence of a shortnose sturgeon has been the sole occurrence of this species in the freshwater portion of a river in the Chesapeake Bay (Welsh et al., 2002; Kynard et al., 2009).

Materials and methods

On 13 March 2016, a gill net was set at river kilometer 48 of the James River (Fig. 1), Virginia, in an attempt to collect juvenile Atlantic sturgeon (under NOAA Endangered Species Permit no. 16547, VCU IACUC#AD20127). The gill net that captured the shortnose sturgeon was 8.3-cm stretch mesh and had a stretched height of 1.8 m. The net was set parallel to the water current and deployed at a depth of 3.2 m. Water quality data at the capture location was determined by using a calibrated YSI Model 85[4] hydrometer (YSI Inc., Yellow Springs, OH). At the sampling location, the temperature was 12°C, dissolved oxygen was 9.89 mg/L, and salinity was 0.04. The net was set for 2 h and pulled during ebb current just before slack water.

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

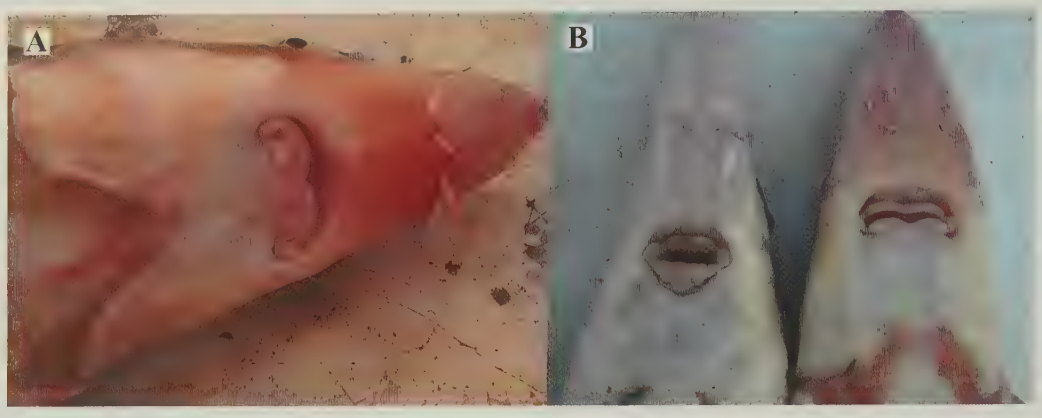

Figure 2

Photographs showing the differences in mouths and noses between the Atlantic sturgeon (*Acipenser oxyrinchus*) and the shortnose sturgeon (*A. brevirostrum*). (**A**) Photograph of the shortnose sturgeon, with an estimated 75-cm fork length, described in this article (photo credit M. Balazik, Virginia Commonwealth University). (**B**) Photograph showing the differences in the mouths and noses of an Atlantic sturgeon (65-cm fork length, left) and a shortnose sturgeon (76 cm fork length, right) (photo credit W. Post, South Carolina Department of Natural Resources).

Results

A sturgeon estimated to be about 75 cm long (in fork length [FL]) was caught during the net set (Fig. 1). This estimated FL reflects the opinion of the experienced researchers and their analysis of photographs that have objects in the background to judge the size of fish. The sturgeon was initially thought to be a subadult Atlantic sturgeon, and standard protocols were followed to process this fish (Kahn and Mohead, 2010). A fin was clipped and taken for genetic purposes, and a passive integrated transponder was placed under the dorsal fin. After the passive integrated transponder was in place, the surface of the fish was noted to be very smooth (Gorham and McAllister, 1974), in contrast with the surface of Atlantic sturgeon. This sturgeon was rolled over to reveal its ventral surface, where pre-anal plates were observed on the ventral median, and the anal fin lacked paired plates (Vecsei and Peterson, 2004). After the placement of plates and smooth skin were noted, it was determined that the fish was most likely a shortnose sturgeon. A picture was taken of the mouth and anal fin, and the fish was released (Fig. 2). No official length measurement of the sturgeon was taken, and the sex was not determined. Genetic analysis verified that the sturgeon caught in the James River was a shortnose sturgeon of the Delaware–Chesapeake Bay stock (King[5]). This collection is the first verified occurrence of a shortnose sturgeon inhabiting the James River.

[5] King, T. 2016. Personal commun. Leetown Science Center, U.S. Geological Survey, 11649 Leetown Rd., Kearneysville, WV 25430.

Shortnose sturgeon mature sexually at approximately 50 cm FL (Dadswell et al., 1984; Bain, 1997); therefore, the fish caught in the James River was likely to have been a mature fish. It was roughly the same size as the 2 gravid females caught in the Potomac River during the Kynard et al. (2009) study. The late-stage shortnose sturgeon caught at river kilometer 63 of the Potomac River was 75 cm FL and was captured on 22 March 2006 (Kynard et al., 2009). The late-stage shortnose sturgeon caught at river kilometer 63 of the Potomac River was 75 cm FL and was captured on 22 March 2006 (Kynard et al., 2009)—at a location and time of capture similar to the documented data for the shortnose sturgeon collected from the James River.

Discussion

The historical occurrence of shortnose sturgeon in the Chesapeake Bay is unclear. Although numerous fin spines from sturgeons were found in the trash middens of Jamestown Colony, none are thought to be from shortnose sturgeon (Balazik et al., 2010). A more intensive study on the scute material from Jamestown Colony is needed to verify or refute this suggestion. The earliest documentation of shortnose sturgeon in the Chesapeake Bay was a partial skin described by Milner in 1876 (Kynard et al., 2009). Uhler and Lugger (1876a) did not list shortnose sturgeon in their first edition of their list of the fish species of Maryland, but this fish was later added to the second edition (Uhler and Lugger, 1876b). During a study of the fish species in the District of Columbia, Smith and Bean (1899) noted that shortnose sturgeon were not as abundant

as Atlantic sturgeon and that commercial fishermen did not recognize the difference between the 2 sturgeon species. Evermann and Hildebrand (1910) and Hildebrand and Schroeder (1927) did not collect any shortnose sturgeon during their studies of the fish of the Chesapeake Bay drainage. Since records were begun in the late 1800s, shortnose sturgeon have seemed to be rare in the upper Chesapeake Bay and nonexistent in the lower Chesapeake Bay, until the capture in 2016 of the individual described here.

There is debate whether the shortnose sturgeon in the Chesapeake Bay are a remnant of a native population that was almost extirpated or are fish from the Delaware River that entered the Chesapeake Bay through the Chesapeake and Delaware Canal (Welsh et al., 2002; Kynard et al., 2009). The Chesapeake and Delaware Canal was completed in 1829; therefore, it is plausible that the shortnose sturgeon described by Milner in 1876 was a colonizing fish from the Delaware River. Welsh et al. (2002) documented shortnose sturgeon traversing the Chesapeake and Delaware Canal. Genetic results support the hypothesis that shortnose sturgeon have strong, distinct genetic lineages that are river dependent (Grunwald et al., 2002; Wirgin et al., 2005, 2010; King et al., 2014), and because shortnose sturgeon rarely leave their natal drainage (Dadswell et al., 1984; Kynard, 1997), one would expect strong genetic diversity for these fish among rivers. Therefore, if shortnose sturgeon captured in the upper Chesapeake Bay are a remnant of a historical population, one would conclude that there would be strong genetic differentiation from shortnose sturgeon in the Delaware River. Considering the extensive sampling efforts by the Virginia Institute of Marine Science, Virginia Commonwealth University, and researchers working with commercial fishermen in all areas of the James River and the lack of any evidence that they have ever documented the occurrence of a shortnose sturgeon in the James River, the one fish described here is not likely to be a member of a remnant population in the James River. The shortnose sturgeon captured in the James River is probably a colonizing or roaming fish from either the Potomac River, about 120 km away, or from the Delaware River, 340 km away, that entered the area through the Chesapeake and Delaware Canal (Fig. 2).

Whether it was a remnant of the Chesapeake Bay or a colonizer from the Delaware River, Kynard et al. (2009) documented a female shortnose sturgeon that exhibited a spawning migration pattern in the Potomac River (Kynard, 1997; Kynard et al., 2009), and it is logical to conclude that shortnose sturgeon are expanding their range into the rivers of the lower Chesapeake Bay. More research is needed to monitor the status and life history of shortnose sturgeon that inhabit all reaches of the Chesapeake Bay. Specifically, the sex of shortnose sturgeon captured in the Chesapeake Bay should be determined, and the fish should be tagged and tracked electronically. The resulting telemetric data will provide managers with the data required to make informed decisions about the current status of this fish in the Chesapeake Bay. Genetic samples should also be taken from every shortnose sturgeon captured in the Chesapeake Bay to help answer the question of whether they are Delaware fish expanding their range or fish from a historical remnant population.

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Spencer F. Baird
First U.S. Commissioner
of Fisheries and founder
of *Fishery Bulletin*

Abstract—We investigated the use of $\delta^{13}C$ and $\delta^{18}O$ stable isotopes in otoliths of juvenile tainha (*Mugil liza*) as indicators of the stock structure of this species of mullet in the southern Atlantic Ocean. Our analysis identified 2 different spawning stocks along the Brazilian coast: the southern stock, from São Paulo (25°S) to Chui (33°S), with distinct seawater temperature requirements for spawning (18–21°C), and the northern stock, from Rio de Janeiro (23°S) to the north (up to 19°S), spawning in seawater temperatures of 21–24°C. These results will contribute to the development of appropriate stock management measures.

Stock identification of tainha (*Mugil liza*) by analyzing stable carbon and oxygen isotopes in otoliths

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The tainha (*Mugil liza*), also known as liza (ITIS, website), is distributed along the coast of South America, from the Caribbean Sea to Argentina (Menezes et al., 2010). The artisanal fisheries for tainha are culturally and historically important along the southern and southeastern coasts of Brazil (Vieira, 1991; CEPSUL[1]). Since the early 2000s, this resource also has been exploited heavily by the Brazilian industrial purse-seine fishery during the reproductive spawning migration of this species (Lemos et al., 2014, 2016) because of the high value of its roe, which is considered a delicacy analogous to caviar (CEPSUL[1]). More recently, strong signs of a decline in numbers have been observed for this species, and, since 2004, tainha have been ranked as overexploited (MPA/MMA[2]). The management plan for this species of mullet (MPA/MMA[2]) is not effective because of a total lack of basic information, including the identification and characterization of the stock or stocks of this fish (Lemos et al., 2016).

[1] CEPSUL (Centro de Pesquisa e Gestão dos Recursos Pesqueiros do Litoral Sudeste e Sul). 2007. I relatório de reunião técnica para o ordenamento da pesca da tainha (*Mugil platanus*, *M. liza*) na região sudeste/sul do Brasil, 67 p. CEPSUL, Itajaí, Brazil. [Available from website.]

[2] MPA/MMA (Ministério da pesca e aquicultura/Ministério do meio ambiente). 2015. Plano de gestão para o uso sustentável da tainha, *Mugil liza* Valenciennes, 1836, no sudeste e sul do Brasil, 137 p. MPA/MMA, Brasília, Brazil. [Available from website.]

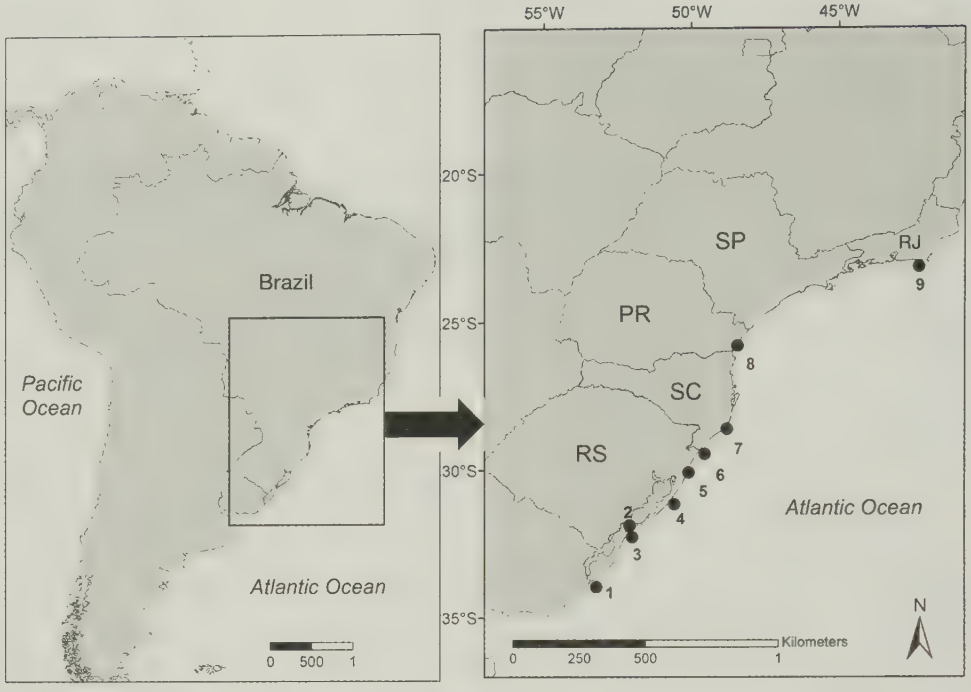

Figure 1

Map of the 9 sampling sites along the coast of southern Brazil where specimens of tainha (*Mugil liza*) were collected in 2011 for this study of the use of stable isotope ratios in otoliths for discrimination of stocks. Sampling sites: 1) Chuí, 2) Patos Lagoon Estuary, 3) Cassino Beach, 4) Mostardas, 5) Tramandaí, 6) Passo de Torres, 7) Laguna, 8) Pontal do Paraná, and 9) Rio de Janeiro. Abbreviations for southwest states: RJ= Rio de Janeiro, SP=São Paulo, PR=Paraná, SC=Santa Catarina, and RS=Rio Grande do Sul.

A stock of fish may consist of a single spawning unit, a biological population, a metapopulation, or various proportions of all these units (Cadrin et al., 2014). The identification of discrete units of stocks has been, for a long time, a basic requirement for fisheries science and management (Cadrin et al., 2014). Many genotypic and phenotypic methods have been applied to identify stocks and distinguish fish populations (Ihssen et al., 1981; Cadrin et al., 2014). In recent years, otolith chemistry has also been used to identify groups successfully on the basis of the characterization of environmental conditions at birth and during early life history stages (Campana et al., 1994; Gao et al., 2001).

The theoretical basis behind stock identification that is based on otolith chemistry is that otoliths are deposited at, or very close to, oxygen isotopic equilibrium with ambient seawater and thus scientists can create a record of the environmental changes that an individual fish experiences through time (Gao et al., 2005). Carbon isotopes deposited in otoliths come from dissolved inorganic carbon (DIC) and animal metabolism, reflecting the physiological status of a fish and trophic changes (Thorrold et al., 1997). The combination of carbon and oxygen isotopes is commonly used to reveal the spatial separation of fish resulting from segregation during spawning, and, therefore, can be used to define populations (Thorrold et al., 1997).

Studies of the biology of tainha along the coast of Brazil have revealed differences among populations that occur over the distribution range of the species and that results from differences in various reproductive parameters (Albieri and Araújo, 2010; González-Castro et al., 2011; Lemos et al., 2014; Mai et al., 2014). For instance, Mai et al. (2014) discovered at least 2 genetically distinct populations between Rio de Janeiro, Brazil, and Mar del Plata, Argentina, that have different reproductive patterns. The southern population is distributed between Argentina and São Paulo, Brazil, and there is the gradual northward migration of tainha from Argentina (at around 37°S) to Santa Catarina, Brazil (at around 26°S). This migration has been reported to occur during a prespawning process that takes place in high-salinity waters (35) and at sea-surface temperatures ranging from 19°C to 21°C, and peak spawning occurs in June (Lemos et al., 2014). About 95% of the commercial catch of this species occurs as fish migrate between the Rio Grande do Sul (33°S) and the Santa Catarina coast (26°S) (CEPSUL[1]).

A traditional and still widely held view regarding stock identification is that fish stocks are reproductively isolated and their own internal dynamics can be identified by genetic markers of lineage (Ihssen et al., 1981). But, the lack of a global molecular marker that identifies a reproductive isolation of fish (Waples et al.,

Table 1

Sites in southern Brazil where juvenile tainha (*Mugil liza*) were sampled in 2011, the number of fish sampled at each site (n), and the mean values of the stable isotopes ratios ($\delta^{13}C$, $\delta^{18}O$), salinity (Sal.), total length (TL), and total weight (TW) of the fish sampled at each site. Standard deviations are given in parentheses.

Sites	n	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	Sal.	TL (mm)	TW (g)
1 Chuí	15	−6.716 (0.71)	0.509 (0.16)	28.5	28.2 (0.88)	0.232 (0.03)
2 Patos Lagoon Estuary	16	−6.793 (0.30)	0.306 (0.20)	7.5	29.5 (0.89)	0.284 (0.02)
3 Cassino Beach	18	−6.709 (0.30)	0.451 (0.23)	27.9	28.6 (1.09)	0.200 (0.01)
4 Mostardas	11	−7.057 (0.26)	0.383 (0.16)	29.1	28.0 (1.01)	0.209 (0.02)
5 Tramandaí	6	−6.774 (0.43)	0.385 (0.13)	30.2	28.3 (1.21)	0.213 (0.03)
6 Passo de Torres	15	−7.169 (0.47)	0.361 (0.18)	11.0	28.0 (1.19)	0.248 (0.03)
7 Laguna	13	−7.323 (0.16)	0.261 (0.11)	31.1	28.0 (0.86)	0.221 (0.09)
8 Pontal do Paraná	3	−7.209 (0.62)	0.320 (0.22)	30.0	28.3 (0.57)	0.270 (0.05)
9 Rio de Janeiro	7	−3.754 (0.51)	−1.141 (0.20)	30.0	28.1 (0.69)	0.217 (0.02)

2008) has led to an approach to identifying stocks and population units that is interdisciplinary. These integrated approaches can provide strong evidences for the identification and delineation of fish stocks (Cadrin et al., 2014). Chemical analysis, for example, provides a greater refinement than genetic analysis alone for identifying a stock (Campana and Thorrold, 2001; Cadrin et al., 2014), and the combination of both approaches is encouraged (Campana et al., 1994; Cadrin et al., 2014).

Our aim was to use isotopic analysis of $\delta^{18}O$ and $\delta^{13}C$ carbonate from otoliths of juvenile fish to test the hypothesis that there is a single stock of tainha within the area where 95% of the commercial catch of this species occurs in southern Brazil.

Materials and methods

Specimens were collected between June and October 2011 at 9 sites along the southern Brazilian coast (Fig. 1) after the reproductive period. One sampling was performed at each of these sites. A beach seine net (9 m long; 1.5 m high) with 13-mm stretch mesh in the wings and 5-mm stretch mesh in the center 3-m section was pulled perpendicular to the beach. Salinity was measured at each sampling site. All fish caught were transported on ice to the laboratory. Individual fish were identified and weighed (in grams), and their total length (TL, in millimeters) was measured.

Differences in the lengths and weights of individuals between the 9 sampling sites were tested by using an analysis of variance (ANOVA). All fish were young-of-the-year ranging in size between 27 and 31 mm TL. Pairs of sagittal otoliths (right and left) were removed from each specimen and sent to the Instituto de Geociências da Universidade de Brasília for analysis. Both whole otoliths were ground to a fine powder, and isotopic ratio mass spectrometry was used for isotopic analysis of carbonates with Vienna Pee Dee Belemnite limestone as the standard.

Differences in the isotopic values among sampled sites were tested by using ANOVA. Isotope values are described by using the standard "δ per thousand (‰)" notation defined as

$$\delta(‰) = (R_{sample} \mid R_{standard} - 1) \times 1000,$$

where $R = {}^{18}O/{}^{16}O$ or ${}^{13}C/{}^{12}C$.

Results and discussion

The values of $\delta^{18}O$ and $\delta^{13}C$ (from −2 to +4‰ and from −9 to +1‰, respectively) found in the otoliths of tainha (n=104) (Table 1) were within the expected ranges for marine species (Kalish, 1991). The isotopic values of the carbon and oxygen revealed 2 groups and therefore the existence of at least 2 stocks (rather than the single stock that we had hypothesized) that have 2 environmentally distinct spawning areas within the overall study area. One group, representing samples taken between the states of Paraná and Rio Grande do Sul, constitutes the southern stock: 0.381‰ (standard error [SE] 0.10) and −6.936‰ (SE 0.46), respectively for $\delta^{18}O$ and $\delta^{13}C$. The second group comprised individuals hatched in the north near Rio de Janeiro: −1.141‰ (SE 0.20) and −3.754‰ (SE 0.51), respectively for $\delta^{18}O$ and $\delta^{13}C$.

The values of $\delta^{18}O$ and $\delta^{13}C$ from Rio de Janeiro and the southern states differed significantly (ANOVA: 23.92 [P<0.0001 and 20.45 (P<0.00001), respectively) (Fig. 2). Homogeneity among values of $\delta^{18}O$ and $\delta^{13}C$ in the samples from the southern states indicates that all individuals from this area were hatched in waters with the same, or very similar, temperatures. Results from analysis indicated an inverse relationship between the environmental temperature and values of otolith $\delta^{18}O$ (Kalish, 1991; Thorrold et al., 1997), revealing that southern individuals were hatched in cooler waters than those waters inhabited by individuals from Rio de Janeiro. On the basis of the relationship proposed

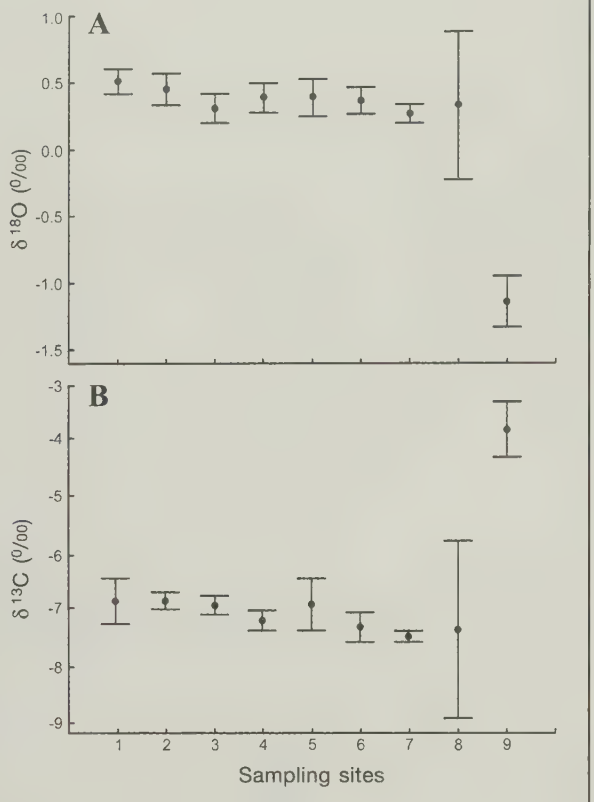

Figure 2

Mean values of (**A**) $\delta^{18}O$ and (**B**) $\delta^{13}C$ of otolith carbonate from tainha (*Mugil liza*) collected at 9 sampling sites: 1) Chuí, 2) Patos Lagoon Estuary, 3) Cassino Beach, 4) Mostardas, 5) Tramandaí, 6) Passo de Torres, 7) Laguna, 8) Pontal do Paraná, and 9) Rio de Janeiro. Error bars indicate standard errors.

by Kalish (1991), $\delta^{18}O$ values from otoliths (–1.141‰ [SE 0.20]) corresponded with water temperature values of 21–24°C, matching the observed sea-surface temperature of the waters off Rio de Janeiro. Similarly, $\delta^{18}O$ values of the otoliths (0.381‰ [SE 0.10]) from southern samples corresponded with water temperature values of 18–21°C, matching the sea-surface temperature at the hatching location of tainha as reported by Lemos et al. (2014).

Lemos et al. (2014) suggested that the peak spawning of the southern population of tainha occurs in June off the coast of the states of Santa Catarina and Paraná. According to our results, this reproductive event provides the annual supply of juveniles of tainha for the entire southern stock. Young-of-the-year disperse southward and are distributed among different nursery areas along the southern coast of Brazil. Vieira (1991) has described the process of dispersion of juvenile tainha along the coast.

The correlation of $\delta^{13}C$ between $\delta^{18}O$ in biological carbonates may indicate kinetic and metabolic effects (McConnaughey, 1989). In otoliths, the correlation between $\delta^{18}O$ and $\delta^{13}C$ is not entirely dominated by kinetic effects, such as it is in corals (Devereux, 1967; Kalish, 1991; Gao and Beamish, 2003). This correlation is induced by biological fractionation and may exhibit different relationships (Gao et al., 2005; Deutsche and Berth, 2006). In contrast to $\delta^{18}O$, $\delta^{13}C$ from otoliths are not in equilibrium with $\delta^{13}C$ values of sea water (Kalish, 1991). About 30% of aragonite carbon is derived from metabolism and is directly related to changes in diet (Kalish, 1991; Gao et al., 2001). The remaining 70% of aragonite carbon comes from DIC (Kalish, 1991). The isotope ratio of otolith carbonate is a mixture of these 2 fractions; therefore, the interpretation of $\delta^{13}C$ is not as straight forward as it is for $\delta^{18}O$ (Kalish, 1991).

As with most species of mullets, for tainha, the ingestion of diatoms and the presence of inorganic sediment in the stomach starts at about 30 mm TL, when juveniles begin to feed near the bottom at the surf zone (Vieira, 1991). There were no significant differences (ANOVA: $P>0.05$) in sizes and weights of individuals among sites (Table 1) that could represent differences in metabolic rates (Campana, 1999). Most of the $\delta^{13}C$ incorporated into the otolith is derived from DIC (Kalish, 1991). The $\delta^{13}C_{DIC}$ may be subjected to small isotopic variations at different latitudes and in different water masses (Kroopnick, 1980; Thorrold et al., 1997). For instance, $\delta^{13}C_{DIC}$ values in the open ocean are fairly uniform, around 1‰; however, in environments with variable freshwater input, $\delta^{13}C_{DIC}$ may vary from –5 to –10‰ (Michener and Lajtha, 2007). The $\delta^{13}C$ values found in our otolith samples (Fig. 2B) indicate that southern waters were influenced by estuarine inputs more than waters near Rio de Janeiro.

Genetic markers provide an important tool for identifying the degree of reproductive isolation between groups (Cadrin et al., 2014). Nevertheless, the study of the life history of an individual fish through otolith chemistry provides fine-scale geographic differences that genetic studies may not be able to detect (Conover, 1998). In our study, there was a great advantage in using phenotypic methods, such as isotope analysis of otoliths, for identifying stocks of tainha. Because the growth patterns of fish groups can be different and strongly influenced by the environment (Campana and Thorrold, 2001) and because fishing acts as a source of recent pressure on evolution (Rijnsdorp, 1993), phenotypic methods are relevant and useful in analyses of fish resources.

Isotopic analysis of $\delta^{18}O$ and $\delta^{13}C$ in otoliths of juvenile tainha revealed 2 stocks along the southern and southeastern Brazilian coasts. The results from this study confirm the observation of Mai et al. (2014) and provide a first biological explanation for the maintenance of genetic difference between these 2 populations. Considering the economic importance of this species for the southern coast of Brazil (from 33°S to 26°S), managers should consider the southern stock as a distinct unit for management purposes.

Acknowledgments

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Effects of recruitment through a coastal hydrodynamic boundary layer on growth and otolith microstructure of larval Gulf menhaden (*Brevoortia patronus*)

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Abstract—Sagittal otoliths (n=208) were removed from larval Gulf menhaden (*Brevoortia patronus*) collected in a Louisiana tidal pass over a 2-year period, from October 2006 to March 2007 and from September 2007 to March 2008, and analyzed with digital imaging and fast Fourier transformations to estimate age and growth. Length at age was estimated by using a 2-cycle Laird–Gompertz growth model and the growth rates were found to be relatively consistent with rates from previous research in the northern Gulf of Mexico, and the estimated timing of an ontogenetic shift in feeding strategy occurred at approximately 33 days after spawning. Laird–Gompertz growth models fitted separately to age and length groupings revealed that the ontogenetic shift was correlated more with larval age than with length. Measurements taken from digital images were used to conduct fine-scale analyses of otolith microstructure and confirmed that a change in otolith structure coincided with the ontogenetic shift in feeding at approximately 33 days after spawning. Keys of length frequencies at age were used to assess temporal variability in Gulf menhaden spawning and they revealed earlier (i.e., September) recruitment to spawning and estuarine areas and shorter recruitment corridors than those previously reported.

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The Gulf menhaden (*Brevoortia patronus*) is both the target of a commercially important fishery in the Gulf of Mexico (GOM; Pritchard, 2005; Vaughan et al.[1]; McCrea-Strub et al., 2011) and is an ecologically important prey item for commercially and recreationally valuable species (Del Rio et al., 2010; Nelson et al., 2012; Simonsen and Cowan, 2013). Gulf menhaden have an established distributional range from the western central Atlantic to the GOM, and specifically within the GOM from Florida Bay to the Bay of Campeche (Whitehead, 1985). The Gulf menhaden fishery is the second largest United States fishery by both weight and value (Pritchard, 2005), and this reduction fishery harvests an average of 400–600 kilotons annually. In recent years, 92% of the annual landings occurred in Louisiana (Vaughan et al.[1]). There is also a second, and minor component of annual landings collected by the small bait fishery in the GOM (VanderKooy and Smith[2]). Although the stock is relatively healthy with a lower fishing-induced mortality rate than that reported for target fishing over the long term, in recent years fishing mortality has increased above the target level, but below the mortality limit, and population fecundity has decreased (Vaughan et al., 2007). Possible limitations to population growth for Gulf menhaden include food availability, habitat limitations, and successful recruitment of larvae into estuarine nursery areas, but with declining recruitment being more of a concern

[1] Vaughan, D. S., J. W. Smith, and A. M. Schueller. 2010. Age, growth and reproduction of gulf menhaden. Southeast Data, Assessment, and Review SEDAR 27-DW02, 34 p. [Available from website.]

[2] VanderKooy, S. J., and J. W. Smith (eds.). 2015. The menhaden fishery of the Gulf of Mexico, United States: a regional management plan, 2015 Revision, 201 p. Gulf States Mar. Fish. Comm., Ocean Springs, MS. [Available from website.]

on the basis of a decrease in population fecundity over the last decade (Vaughan et al., 2007).

Gulf menhaden are estuarine dependent and reportedly spawn from October through February (Whitehead, 1985; Nelson and Ahrenholz, 1986; Vaughan et al., 2000) and the peak estuarine recruitment occurs in late January and early February (Lewis and Roithmayr, 1981; Shaw et al., 1988). Spawning depth for Gulf menhaden is usually 90 m and shallower (Whitehead, 1985; Powell, 1994), and spawning locations occur farther offshore as the season progresses, suggesting shorter "recruitment corridors" (Cushing, 1975) during fall recruitment (Vaughan et al., 2007). Mean egg diameter has been reported to be 1.61 mm, and length at hatching to be approximately 3 mm total length (Dahlberg, 1970; Lewis and Roithmayr, 1981; Shaw et al., 1985). The pelagic eggs take 2–3 days to hatch and another 2–3 days until yolk absorption is complete, with the result that first feeding and first otolith increment formation occur approximately 5 days after spawning (Warlen, 1988). Offshore larval drift and cross shelf transport have been reported to take between 4 and 10 weeks (Shaw et al., 1988). The variability in transport times is tied to the limited swimming capacity of larval fish (Shanks and Eckert, 2005); successful estuarine recruitment is therefore driven more by oceanographic flows (Guillory et al., 1983; Epifanio and Garvine, 2001; Gillanders et al., 2003). Recruitment from more oligotrophic inner continental shelf spawning grounds through the hydrodynamically variable oceanographic coastal boundary layer, which is produced by atmospheric effects, into tidal passes, and ultimately more productive estuarine waters (Raynie and Shaw, 1994) corresponds with the time period when Atlantic menhaden (*Brevoortia tyrannus*) and Gulf menhaden larvae transform from selective particulate feeding to omnivorous filter-feeding juveniles (Stoecker and Govoni, 1984; Deegan, 1990; Chen et al., 1992; Lozano et al., 2012). This transformation begins at approximately 20 mm standard length (SL) and is completed by approximately 30 mm SL (Hettler, 1981; Warlen, 1988), with a corresponding increase in gill raker counts. For example, gill raker counts were recorded to increase from 5 +14 to 13 +25 for larvae between 19 and 22 mm SL, as they were beginning to undergo metamorphosis in Lake Pontchartrain, Louisiana (Suttkus, 1956).

Studies of larval Gulf menhaden age and growth in Louisiana have focused on both the offshore (Shaw et al., 1985, 1988; Warlen, 1988; Raynie and Shaw, 1994) and inshore components of the recruitment corridor (Deegan and Thompson, 1987; Marotz et al. 1990; Raynie and Shaw, 1994). These studies have reported growth rates between 0.28 and 0.42 mm/day for the smaller larvae typically encountered on the continental shelf (Deegan and Thompson, 1987; Raynie and Shaw, 1994) and between 0.11 and 0.12 mm/day for larvae collected within Sabine Pass and Fourleague Bay, Louisiana (Warlen, 1988; Raynie, 1991).

Daily growth increments in otoliths have been confirmed in larval Gulf menhaden in laboratory studies (Warlen, 1988). The daily rings in otoliths of larval fish can provide growth rates and can act as a proxy for identification of changes in developmental stages and for environmental stress reflected in the variability in otolith ring width (Maillet and Checkley, 1990, 1991; Chambers and Miller, 1995). Analysis of larval otolith structure was initially done by visual inspection; however, video and digital methods have become prevalent with an increase in computing resolution and digital imaging (Ralston and Williams, 1989; Campana, 1992; Morales-Nin et al., 1998). Regardless of what ring counting method is being used, the ring structure must be verified because the shape and relative size of otoliths are species specific and genetically controlled (Schmidt, 1969; Gaemers, 1976; Nolf, 1985; Lombarte and Morales-Nin, 1995; Morales-Nin et al., 1998).

The objectives of our study were as follows. First, to determine the length at age of Gulf menhaden for the sampling period. Second, to determine at what age there is a shift in growth rate consistent with the expected shift in feeding strategy from a selective particulate feeder to an omnivorous filter feeder. Third, to compare otolith microstructure with length at age models for confirmation of growth rate and shift in feeding strategy upon entering the coastal boundary layer and the transition from oceanic to estuarine waters. Fourth, to determine the distribution of the spawning period by using back calculation of spawning dates from age frequency keys. Fifth, to determine the duration of the recruitment corridor from offshore spawning grounds across the coastal boundary layer, and into the estuarine nursery grounds.

Materials and methods

Sampling location

Samples of ichthyoplankton were collected near the Port of Fourchon, in Bayou Tartellan, Louisiana (Fig. 1). This sampling location is connected to the GOM at Belle Pass (29°5′53.9″N, 90°13′17.8″W) and is one of the first major inland bifurcations of the tidal pass. The tidal pass and Bayou Tartellan are seasonally well mixed and have limited temperature, salinity, or dissolved oxygen stratification. Bayou Tartellan is also characterized by high turbidity, and a low volume of freshwater input owing to a limited drainage basin. The sampling location (29°6′49″N, 90°11′4″W) was determined to maximize flow rates for passive sampling of the tidal pass. The passive sampling was conducted from the end of a 3.7-m-long dock on the northern bank of the tidal pass, which had a sampling depth of 10 m and an overall tidal pass width of approximately 73 m.

Field methods

Individual samples of ichthyoplankton were collected passively with a 60-cm ring net (with 333-μm mesh, and 2 m in length) that was dyed dark green to mini-

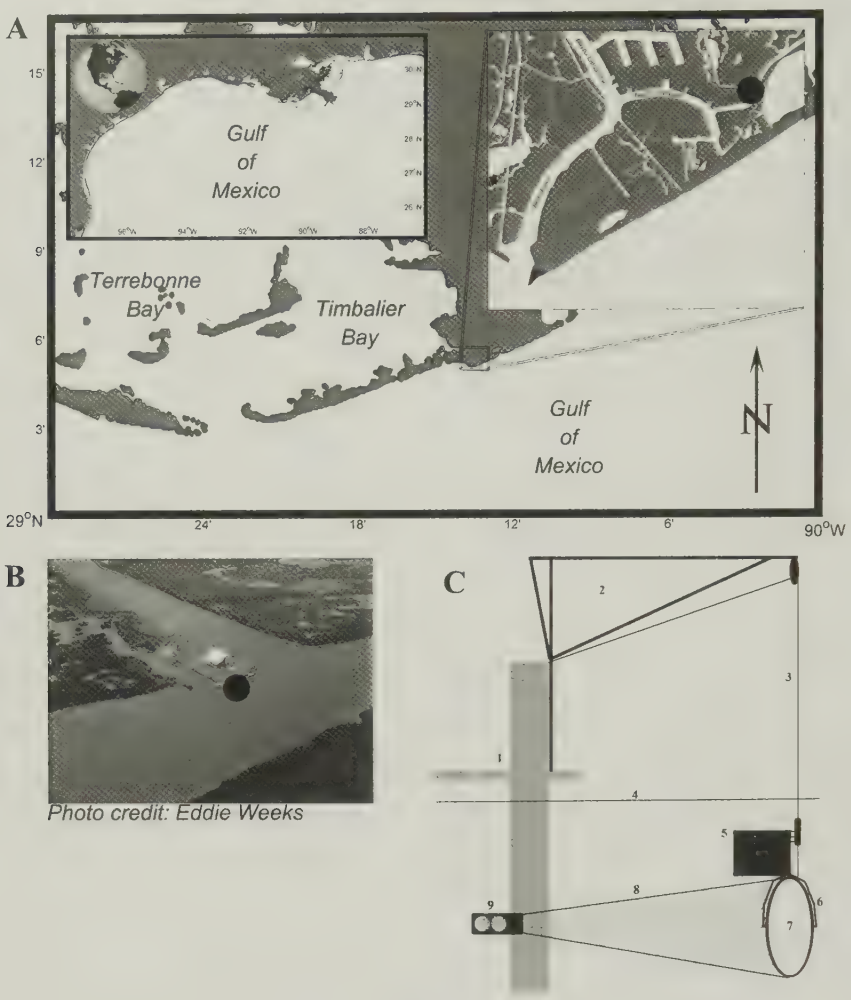

Figure 1

(**A**) Map of the sampling location for this study in relation to the Gulf of Mexico and coastal Louisiana. The upper right inset represents the area around Port Fourchon, Belle Pass, Louisiana, and the sampling site in Bayou Tartellan identified by a black circle on the map. Sampling for larval Gulf menhaden (*Brevoortia patronus*) was conducted from October 2006 through April 2007 and again from September 2007 through April 2008. (**B**) Aerial photograph of the sampling site at Bayou Tartellan; the black circle again identifies the sampling site. (**C**) Diagram of the sampling system: 1) fixed dock where the sampling system was attached, 2) davit that was used to extend the net farther into the channel, 3) cable system by which the net was raised and lowered, 4) water surface, 5) orientation vane for the net system, 6) 60-cm metal ring that held open the net mouth, 7) pivoting gimbal, 8) 333-µm mesh net, dyed dark green, and 9) plastic, vinyl-coated codend with 333-µm drainage ports.

mize avoidance of the net. The ring net was outfitted with a gimbal and current vain for proper net orientation. The net system was raised and lowered for sampling and collection of samples by using a fixed davit, from which was suspended a stainless steel cable from above the sampling deck to the channel bottom. Samples were collected by using a plastic vinyl coated codend with 333-µm-mesh drainage ports attached to the end of the net. To determine the volume of filtered water, a flowmeter (model no. 2030; General Oceanics Inc.[3], Miami, FL) was positioned slightly off center of the ring to determine the volume of water filtered.

Samples were collected every 4 h over a 72-h period, twice monthly between the months of October and April, over a 2-year period (2006–2008), except during December and January, which were sampled

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

only monthly. In addition, 2 sampling efforts occurred in September 2007. The sampling design was developed to focus on atmospheric cold front passages, which are intermittent wind-dominated meteorological events common from the late fall through early spring along the Louisiana coast. Individual sampling dates were chosen to maximize sampling during astronomical tidal ranges to better evaluate the potential impacts of these atmospheric events. Ichthyoplankton were collected randomly and passively from both the surface and near-bottom. Collections at the surface were 6 min in duration, and net samples collected near-bottom were 10 minutes. These differences in sampling duration were chosen to attempt to have similar volumes of water filtered through the net. To prevent contamination of the net during deployment for near-bottom sampling, the net mouth was closed until the ring net was at depth, and was closed again after sampling for retrieval. Nets were rinsed and washed down with fresh water to avoid sample contamination. All ichthyoplankton sampling was conducted under pre-approved planning and authorization by the Institutional Animal Care and Use Committee.

Ichthyoplankton samples were initially preserved in 10% buffered (sodium phosphate, dibasic $NaH_2PO_4 \cdot H_20$ and monobasic Na_2HPO_4) formalin—a short-exposure, long-term fixative—for approximately 3.5 h. Samples were then rinsed and transferred to a 70% ethanol solution for long-term storage and for later examination of the larval fish otoliths.

Estuarine hydrographic parameters were measured at dockside during each plankton sampling event by using a portable YSI Model 85 instrument (YSI Inc., Yellow Springs, CO) to collect data on temperature, conductivity (salinity), and dissolved oxygen at each depth during net deployment. Data concerning predicted diurnal tides, measured tide height, and the resulting alteration in the expected tidal prism were collected from a nearby tide gauge station (station ID: 8762075; NOAA Tides and Currents, website) at the Port of Fourchon, Belle Pass, Louisiana (29°6.8′N, 90°11.9′W).

Laboratory methods

A Motodo Plankton Splitter (Aquatic Research Instruments, Hope, ID) was used to split samples with volumes greater than 200 mL in half and to split samples with a volume greater than 400 mL into quarters. All ichthyoplankton were removed from the samples and placed into 10-mL scintillation vials by using a dissecting stereoscope. To ensure that all ichthyoplankton were removed, a random subset of samples from both surface and near-bottom collections were checked by a second party after initial processing.

Ichthyoplankton were identified to the lowest taxonomic classification possible; however, size and physical condition were potentially limiting factors for definitive confirmation of identification. Alizarin blue and alizarin red were used to confirm meristic counts for individual ichthyoplankton that were difficult to identify. Gulf menhaden larvae were separated and stored in 70% ethanol for otolith analysis. Identifications of larval fish were based on identification guides by Richards (2005) and Fahay (2007).

Gulf menhaden were subsampled from each surface and near-bottom sample for otolith analysis on the basis of the normal distribution of SL of all Gulf menhaden larvae collected. Measurements of SL to the nearest 0.1 mm were taken with a Leica MZ6 stereoscope (Leica Microsystems, Buffalo Grove, IL) calibrated against a microscope stage micrometer. Gulf menhaden larvae were subsampled from every sampling effort that contained the target species. In samples where 3 or fewer Gulf menhaden larvae were collected, all larvae were selected for otolith removal. In samples that contained more than 3 Gulf menhaden larvae, 3 larvae were selected so that a larva with the longest SL, shortest SL, and a SL from the normal distribution was chosen for otolith removal. Removal, preparation, analysis and otolith interpretation were undertaken according to the methods described in Kupchik and Shaw (2016).

Age determination and spawning dates

Age of larval gulf menhaden, recorded in days after spawning (das), was determined from the counts of growth increments (otolith radii) by using a semi-automated image analysis method (Kupchik and Shaw, 2016). Daily increment deposition has been confirmed to have an increment-count to age-regression slope of 1 for larval Gulf menhaden growth (Geffen, 1992). As with the method used by Raynie (1991), we applied a 5-day lag for the first increment formation after spawning for Gulf menhaden larvae on the basis of laboratory research (Warlen, 1988). This lag resulted in a calculation of total age das where 5 days were added to the number of increments from read otoliths. For modeling growth, we applied a 3-day lag for first increment formation after hatching (Warlen, 1988). This resulted in a calculation in total age in days after hatching (dah) where 3 days are added to the number of increments determined from otolith reading. Ages were estimated for larvae not selected for dissection by using frequency of age-at-length keys and the FSA package, vers. 0.7.4, for R software, vers. 3.1.1 (R Core Team, 2014).

Spawning dates were calculated for all Gulf menhaden larvae; direct calculation was made for those larvae where otolith radii were analyzed, and also for those where the age was estimated with the method described by Isermann and Knight (2005), namely with a semi-random method in the FSA package. The spawning date was determined as the difference between the date of capture and the age in days after spawning.

Growth rates

Distributions of lengths and calculated ages based on increment counts were tested for normality by using a Shapiro–Wilk's test. Instantaneous larval growth (per

day) is expected to be fastest soon after first feeding, to decrease thereafter, and a large decrease or growth stanza is associated with an ontogenetic shift in feeding from selective particulate feeding to omnivorous filter feeding (Deegan, 1990; Lozano et al., 2012) in combination perhaps with transgressing the coastal boundary layer. To represent this shift in feeding strategy between the larval and juvenile stages, a derivative of the Gompertz model (Gompertz, 1825) was chosen because it highlights this specific pattern of growth. Larval somatic growth of Gulf menhaden was modeled by applying only the directly analyzed otolith data to a 2-cycle Laird–Gompertz growth model (Laird et al., 1965; Zweifel and Lasker, 1976; Raynie, 1991), and fitting the model with the use of R software. The 2-cycle Laird-Gompertz growth model is represented by the following equation:

$$L_t = L_{null} e^{\left[\frac{\gamma(1 - e^{(-\alpha\Delta_1)})}{\alpha} + \frac{\delta(1 - e^{(-\beta\Delta_1)})}{\beta}\right]}$$
$$\Delta_1 = MIN(t, t^*), \text{and} \quad (1)$$
$$\Delta_2 = MAX(t - t^*, 0),$$

where L_t = the SL (in millimeters) at age (dah);
L_{null} = SL at hatching for Gulf menhaden; and
$\gamma = \frac{A}{\alpha}$
where A = the age specific instantaneous growth rate at spawning;
α = the rate of exponential decay in growth rate before t^*;
t^* = the time at which there is a shift between somatic growth stages;
$\delta = \frac{B}{\beta}$
where B = the age specific instantaneous growth rate immediately after the stage shift at $t = t^*$; and
β = the exponential decay in growth in B.

The length at hatching was estimated but was based on literature. To increase model speed, length at hatching was constrained between 1 and 4 mm on the basis of the literature reporting between 2 and 4 mm (Hettler, 1981; Warlen, 1988; Powell, 1994; Raynie and Shaw, 1994). Similarly, t^* was estimated with a lower bound constraint of 20 dah, and an upper bound constraint of 45 dah (Suttkus, 1956; Hettler, 1981; Raynie, 1991). Hind-casting to estimate growth rates for larvae at ages not sampled, owing to larvae being offshore at these early ages, can be accomplished by using this 2-cycle Laird–Gompertz growth model (Lozano et al., 2012). The 2-cycle Laird–Gompertz model was applied to the pooled otolith data, and to each of the 2 sample years. Comparison between the yearly and pooled models was conducted with an F-test in R software.

The Laird parameterization of the Gompertz growth model was applied to both the pre-ontogenetic transformation period and the postontogenetic transformation period for groupings based on SL from the distribution of SLs of larvae whose otoliths were examined and based on the estimated transformation age from previous literature (Raynie, 1991). The Laird-Gompertz model was fitted by using R software and took the following form:

$$L_t = L_{null} e^{k(1 - e^{-at})}, \quad (2)$$

where L_t = the SL (in millimeters) at age t (days);
L_{null} = SL at hatching for Gulf menhaden;
a = the rate of exponential decay; and
k = a dimensionless parameter so that ka represents the instantaneous growth rate at hatching.

Hind-casting can also be used to estimate growth rates for larvae at ages not sampled with this model structure (Lozano et al., 2012).

Changes in the magnitude of growth rate were measured by using differences in the width of the daily increments and variation in ring distance from the otolith core. Changes in otolith ring width and distance from the core are expected to occur after the ontogenetic shift in feeding strategy. Ring width was measured with the method described by Kupchik and Shaw (2016), and mean ring distance from the core and mean ring width were calculated for both the sampling period from October 2006 to March 2007 and the period from September 2007 to March 2008.

Results

Hydrology

Water temperatures based on sampling depth yielded no statistical differences—a result that is consistent with a seasonally, vertically well-mixed tidal pass. Water temperatures (mean: 20.5°C) generally had low variability during any sampling effort. However, from late November 2006 to early February 2007, recorded temperatures were colder and fluctuations were greater than those during other sampling efforts. In particular, the January 2007 sampling had a maximum difference of 10.2°C during the 72-h sampling period. Water temperatures were warmer during September and October, cooled from November through February, and then began to warm again in March and April. During November 2006, there was a large decrease in water temperature, and median water temperatures for each sampling effort remained below 15°C until early February 2007. In November 2007, there was also a decrease in water temperature; however, median water temperatures remained higher than 17°C for all subsequent sampling efforts.

Seasonality of larval Gulf menhaden collections

There were 2846 Gulf menhaden larvae collected in Bayou Tarellan during the sampling efforts from October 2006 to April 2008; 2158 larvae were collected during year 1, October 2006 to March 2007, and 688 larvae were collected during year 2, September 2007 to March

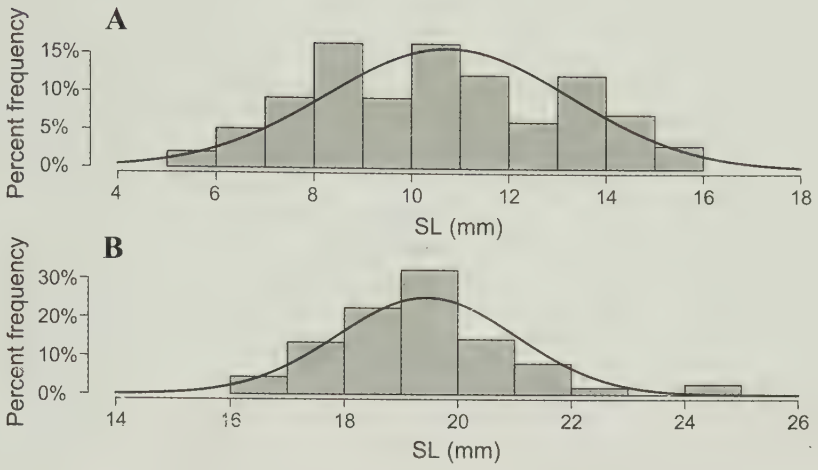

Figure 2

Histograms of standard length (SL) data for all Gulf menhaden (*Brevoortia patronus*) larvae collected at Bayou Tartellan, Louisiana, from October 2006 to April 2007 and from September 2007 to April 2008 and that were used in analyses of sagittal otoliths: (**A**) all larvae between 5 and 16 mm SL, mean: 10.9 mm (SD 2.51), and (**B**) all larvae greater than 16 mm SL, mean: 19.4 mm (SD 1.39). Both histograms were normally distributed (Shapiro–Wilk's test: $P>0.05$).

2008. January 2007 accounted for 40% of all larvae collected during the period from October 2006 to March 2007, and 30.3% of the total number of Gulf menhaden larvae were collected over both years. November 2007 collections had the second highest number of larvae, accounting for 26.3% of all Gulf menhaden larvae collected in year 2, and 6.4% of all larvae collected across both sampling years.

Length, age, and spawning dates

There were a total of 240 Gulf menhaden larvae that had sagittal otoliths removed for analysis. Thirty-two otoliths did not produce readable radii and were excluded from analysis. The length frequency of all larval Gulf menhaden that were aged (n=208) did not follow a normal distribution (Shapiro–Wilk: $P<0.0001$). As a result, we split the overall distribution into 2 groups to achieve 2 normal distributions, one of larvae between 5 and 16 mm SL (mean: 12.1 mm SL [standard deviation (SD) 3.71]) and the second consisting of larvae greater than 16 mm SL (mean: 19.4 mm SL [SD 1.39]; Fig. 2). The mean SL in year 1 was 14.7 mm (SD 4.61), and the mean SL for year 2 was 16.3 mm (SD 4.83), with a slightly larger range. Overall, the largest larvae were collected from January through March. In year 1 the largest larvae were collected in January 2007, in year 2 the largest larvae were collected in March 2008.

Combining both sample years, larval Gulf menhaden had a mean age of 32.3 das (SD 12.15), a median of 31.5 das, and a range of 11–67 das. For year 1, October 2006 to March 2007, the ages ranged from 15 to 67 das, and a maximum density between 18 and 24 das. Also in year 1, the oldest larvae were collected in the largest numbers between December 2006 and February 2007. In year 2, September 2007 to March 2008, the highest densities were for larvae between 35 and 45 das, and the oldest larval Gulf menhaden were collected in March 2008.

In both sampling years, approximately half of all spawning dates for larvae sampled in Bayou Tartellan occurred before mid-January, and the other half occurred later in the year. In year 1, the greatest number of spawning dates occurred from 1 to 28 February 2007, and a smaller secondary peak occurred in October 2006 (Table 1). During year 2, the greatest number of spawning dates occurred between 16 January and 15 February 2008, and a second smaller peak occurred in late October or early November 2007.

Gulf menhaden growth rates

The 2-cycle Laird-Gompertz growth model provided a model fit that accounted for a faster initial growth rate and for a slower growth rate after the ontogenetic change (Fig. 3). The shift in growth rate and feeding pattern was estimated in the model to occur after 31 dah (t^*=31.086), or 33 das. The model estimated that length at hatching was 3.34 mm SL, and an age-specific growth rate at hatching of 0.0014/day. During this larval stage, the maximum growth rate was 0.72 mm/day, and mean growth rate was 0.47 mm/day. After the start of the developmental shift, at the modeled SL of 17.88 mm, the age-specific growth rate was 0.0006/day. The

Table 1

Spawning intervals for larval Gulf menhaden (*Brevoortia patronus*) collected in Bayou Tartellan, Louisiana, during 2006–2008. Spawning dates were determined from back-calculated otolith ages and collection dates after application of age–length keys. Percentages of the total number of larvae collected in each sampling year and cumulative percentages for each sampling year are based on half-month intervals.

Interval	2006–2007		2007–2008	
	%	Cumulative %	%	Cumulative %
09/01–09/15	0.07	0.07	0.20	0.20
09/16–09/30	1.39	1.46	0.40	0.61
10/01–10/15	15.28	16.74	1.97	2.58
10/16–10/31	8.45	25.19	9.91	12.49
11/01–11/15	2.95	28.14	10.12	22.61
11/16–11/30	2.49	30.63	4.86	27.47
12/01–12/15	6.79	37.42	11.33	38.80
12/16–12/31	9.70	47.12	8.50	47.29
01/01–01/15	2.49	49.62	5.92	53.21
01/16–01/31	6.58	56.20	14.67	67.88
02/01–02/15	20.96	77.17	19.47	87.35
02/16–02/28	19.13	96.29	7.28	94.64
03/01–03/15	2.25	98.54	3.95	98.58
03/16–03/31	1.46	100.00	1.42	100.00

initial portion of this growth stanza had a maximum growth rate of 0.21 mm/day, and an average growth rate of only 0.11 mm/day. The 2-cycle Laird–Gompertz models were also fitted separately to year 1 (October 2006 to March 2007) and year 2 (September 2007 to March 2008); however, these 2 models did not result in better performance over the pooled model (F-test: P=0.201; Fig. 3).

Individual Laird–Gompertz models were fitted for pre- and postmetamorphosis, first where the stages are delineated by age, and secondly where the stages are determined from SL. The breakdown by age between the 2 Laird–Gompertz models provided better fits in describing somatic growth during each period in contrast with the grouping determined by SL because of the increased variability in length at a particular age. The first Laird–Gompertz model for larval stage based on age groupings had an initial specific growth rate of 0.072/day, and a weaker decay rate of 0.019. This larval stage had a modeled maximum growth rate of 0.71 mm/day, and a mean growth rate of 0.47 mm/day (Fig. 4A). During the initial portion of the transition to the juvenile developmental stage, the decay rate for the age-grouped model was 0.051. This stage in the age-grouped model had a maximum growth rate of 0.20 mm/day, and an average growth rate of 0.08 mm/day. The premetamorphic larval stage for the SL grouping had an initial specific growth rate of 0.086/day, and a decay rate of 0.041. This premetamorphic stage had a modeled maximum growth rate of 0.41 mm/day, and a mean growth rate of 0.38 mm/day (Fig. 4B). At the onset of metamorphosis to the juvenile developmental stage, the decay rate was 0.015. The very beginning of the ontogenetic shift to the juvenile developmental stage had a comparatively lower maximum growth rate of 0.12 mm/day, and an average growth rate of 0.10 mm/day.

Analyses of otolith microstructure showed changes in both mean ring distance from the otolith core, as well as in mean ring width after 33 das. Mean ring distance from the core during the initial larval stage was similar for both October 2006 to March 2007 and September 2007 to March 2008. After the beginning of the model-estimated ontogenetic shift at approximately 33 das, otolith growth slowed and showed limited variability, and year 2 otolith growth was slower than that of year 1 (Fig. 5A). Mean ring width showed a similar pattern: a decline in ring width occurred after 33 das and limited differences between either sampling years. Before the beginning of the ontogenetic shift onset, ring width for both sample years appeared to increase slightly, agreeing with the 2-cycle modeled growth rate that was largest just before the expected onset of shift in feeding strategy (Fig. 5B).

Discussion

Hatching length as calculated by the 2-cycle, Laird–Gompertz model was 3.34 mm, which agreed well

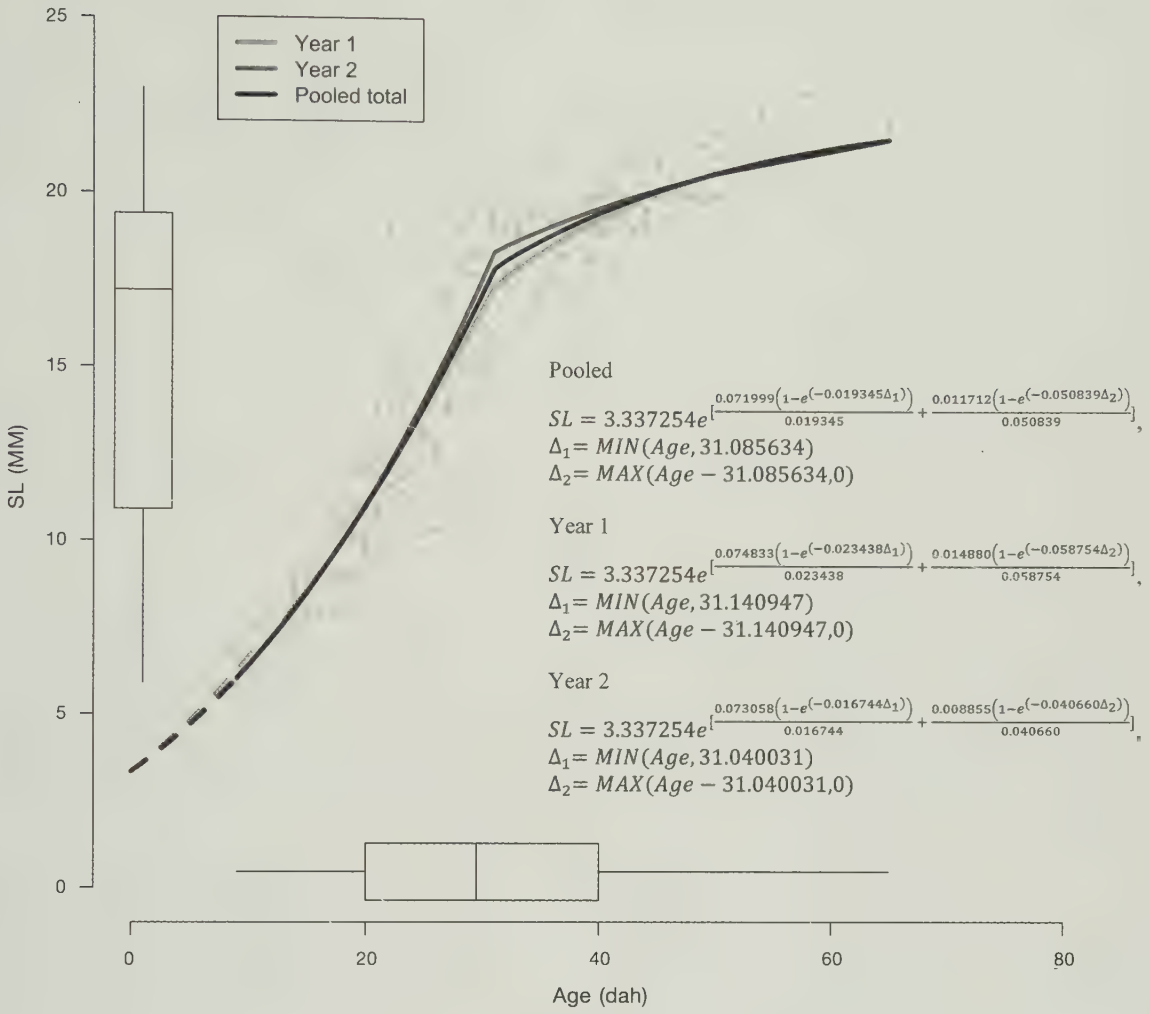

Figure 3

Relationships of standard length (SL) to age in days after hatching (dah) estimated with 2-cycle Laird–Gompertz growth models for each sampling year and a pooled total of data from otoliths of larval Gulf menhaden (*Brevoortia patronus*) collected at Bayou Tartellan, Louisiana, from October 2006 to April 2007 and from September 2007 to April 2008. The dashed lines represent the hind-casted models through the estimated intercept to estimate growth rates of larvae at ages in dah less than the minimum age measured. Boxplots show the median, 25%, and 75% quantiles, 95 percent confidence intervals, and outliers are provided for each axis. The 2-cycle Laird–Gompertz models were parameterized with equations provided in the figure.

with approximately the 3 mm total length reported elsewhere (Hettler, 1981; Warlen, 1988; Powell, 1994; Raynie and Shaw, 1994). Smaller and younger larvae were encountered earlier during the sample period (i.e., September to early October) for both years. Early September estuarine recruitment of Gulf menhaden larvae is novel for Louisiana waters (Raynie and Shaw, 1994; Carassou et al., 2012), and the smaller sizes and younger ages suggest a truncated recruitment corridor and spawning that occurs earlier than previously reported and within more coastal waters (Shaw et al., 1988). The shorter distance of the spawning ground to estuary recruitment corridor at this time of year may possibly be a result of the influences of the offshore GOM hypoxia zone that shifts spawning aggregations into a narrow, alongshore corridor (Vaughan et al., 2007). Although there is still much debate on the role that hypoxia may play in fisheries production (Chesney and Baltz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008), such a shortened spawning-ground to estuary-recruitment corridor, may drive earlier estuarine recruitment for larval Gulf menhaden, thereby decreasing offshore mortality during larval drift (Cushing, 1974; Letcher et al., 1996).

Spawning dates back calculated from ages (das) suggested movement of spawning aggregations far-

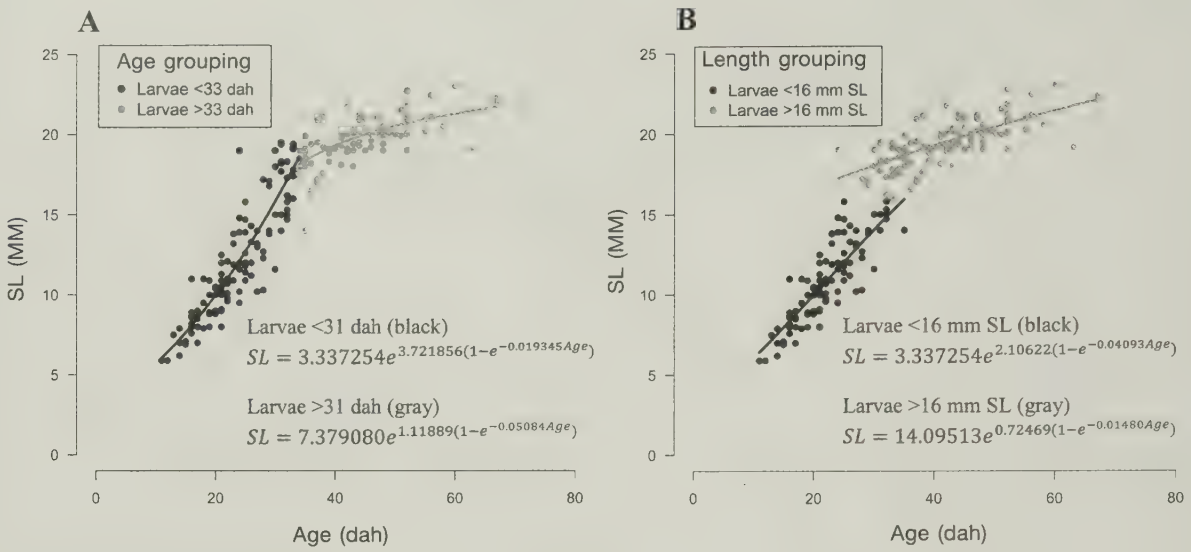

Figure 4

Relationships of standard length (SL) to age in days after hatching (dah) estimated with Laird–Gompertz growth models for each grouping of data from analysis of larval Gulf menhaden (*Brevoortia patronus*) collected at Bayou Tartellan from October 2006 to April 2007 and from September 2007 to April 2008 (**A**) For the age grouping, larvae with a measured age less than 31 dah are indicated as points in black with the corresponding black model line, and larvae greater than 31 dah are indicated as points in gray with the corresponding gray model line. (**B**) For the length grouping, larvae with a measured SL less than 16 mm are indicated as points in black with the corresponding black model line, and larvae greater than 16 mm SL are indicated as points in gray with the corresponding gray model line. Model parameterizations were calculated with the equations provided in the figure.

ther offshore as the season progressed (Whitehead, 1985; Vaughan et al., 2007). Spawning was bimodal in both years and peaked during fall in either October or November, depending on year. This peak was smaller than the second, late-winter peak, which occurred in either late January or early February for years 1 and 2, respectively. This large second spawning peak is consistent with previously reported spawning peaks that occurred in late January and February (Shaw et al., 1988; Powell 1994; Raynie and Shaw, 1994; Vaughan et al., 2000). In particular, collection of small (3–5 mm SL) and young (7–12 das) larvae in late September to early October had back-calculated spawning dates that suggested a much earlier spawning season (i.e., September) and a much shorter recruitment corridor than previously reported. Overall, the larvae of the fall spawning peak were generally smaller (mean: 14 mm SL), and younger (22 das) than the larvae that composed the winter peak (mean: 19 mm SL; age: 41 das). The fall peak, however, corresponded with a shorter recruitment corridor and transit time (i.e., approximately 3 weeks) compared with the winter peak with transport times of approximately 6 weeks. The fall transit time, therefore, is much shorter than the transport time of 4–10 weeks estimated by Shaw et al. (1988) but corresponds well with adults being distributed along the coast in nearshore waters during late summer or early fall before moving farther offshore in October (Ahrenholz, 1991) and perhaps being somewhat constrained by the Louisiana hypoxic zone (Vaughan et al., 2007).

The greatest larval growth rate was determined to occur a few days before the beginning of the ontogenetic transformation from a selective particulate feeding to omnivorous filter feeding, and during the shift from oceanic waters through the coastal boundary zone into the estuary, but there was some variability between sampling years. The 2-cycle Laird–Gompertz model estimated a maximum growth rate for the initial larval stage of 0.72 mm/day at 33 das, which was similar to the individual age-grouped Laird–Gompertz model of 0.71 mm/day at 33 das, and both models had higher maximum growth rates than those estimated with the SL-grouped Laird–Gompertz model (0.41 mm/day). The individual Laird–Gompertz models grouped by SL showed agreement and had a mean calculated growth of 0.38 mm/day that agrees with previously reported values of 0.36 mm/day (Raynie, 1991) and 0.37 mm/day (Warlen, 1988). However, the agreement among the 2-cycle Laird–Gompertz models in our study, the individual Laird–Gompertz models grouped by age, and the results by Raynie and Shaw (1994), suggests that timing of the onset of metamorphic development is tied to age and ultimately ontogeny based on shifting prey fields (Ditty, 2002). Any differences in length at

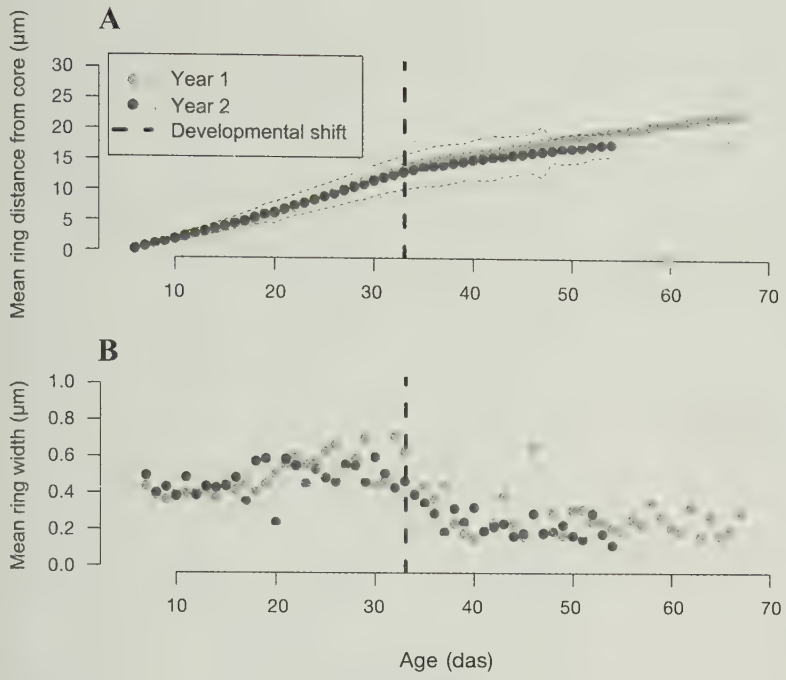

Figure 5

Data from analysis of otolith microstructures of larval Gulf menhaden (*Brevoortia patronus*) collected at Bayou Tartellan, Louisiana, from October 2006 to April 2007 (year 1) and from September 2007 to April 2008 (year 2). (**A**) Otolith ring mean distance from the core by sample year. The vertical black dashed line represents the modeled developmental shift, at 33 days after spawning (das), from the larval stage into the beginning of the juvenile stage. The thin dashed lines represent 95% confidence intervals for the measured distances. (**B**) Mean ring width for individual daily rings observed in otoliths. Decreases in ring width correspond with the modeled developmental shift that occurred at 33 das.

these ages is likely to be due to the variability of food sources or other resources that result in differences in the instantaneous larval growth rate (Warlen, 1988; Lyczkowski-Shultz et al., 1990; Warlen, 1992) during the initial larval stage, when Gulf menhaden larvae are selective particulate feeders (Stoecker and Govoni, 1984; Deegan, 1990; Lozano et al., 2012).

Differences in water temperature between sampling year 1 and 2 are correlated with the slight differences in growth rate and otolith microstructure between both years. In year 1 the highest growth rate was 0.63 mm/day and was much lower than the maximum growth rate in year 2 (0.77 mm/day), when overall warmer water temperatures likely aided increased somatic growth (Houde, 1974; Heimbuch et al., 2007). However, differences in mean ring distance from the otolith core, although small, showed the opposite trend, with slightly faster otolith ring growth during year 1. Previous research has revealed a similar decoupling between otolith growth and somatic growth (Mosegaard et al., 1988; Fey, 2006). Despite this partial decoupling, otolith microstructure for both years showed an increase in otolith ring width directly before the beginning of the ontogenetic shift from selective particulate feeding to omnivorous filter feeding—an increase that suggests a direct relationship between the ontogenetic shift and otolith deposition. The high growth rate before the shift in feeding strategy may be the result of a cumulative experience of adjusting to food source or environmental resources, before learning new feeding skills to accommodate the ongoing development of new feeding structures (Stoecker and Govoni, 1984; Deegan, 1990; Maillet and Checkley, 1990; Lozano et al., 2012).

There was overwhelming agreement with the pooled 2-cycle Laird–Gompertz model, with the fit of the 2-cycle Laird–Gompertz models for each individual year, and with the otolith microstructure analysis, for the mean age for the shift in growth. This growth stanza is a reflection of 1) transitioning from offshore spawning grounds through the coastal boundary layer and to an estuarine water mass with differing primary productivities and 2) the onset at which the ontogenetic shift from the larval stage to the juvenile stage begins. The modeled shift in growth (33 das) coincides with the previously reported shift in growth rate at 33.6 das for Gulf menhaden in Fourleague Bay, Louisiana (Raynie and Shaw, 1994). Mean distance from the otolith core and mean ring width decreased after 33 das, which probably reflects limited feeding at this point owing to the ontogenetic shift (Deegan, 1990; Raynie, 1991; Warlen, 1992; Lozano and Houde, 2013). Transforming larvae at this age, which were between approximately 19 and 21 mm SL, may be expending more energy in the development of a feeding apparatus as they change food source for the juvenile and adult stage (Deegan, 1990; Maillet and Checkley, 1990), and in deepening their body rather than increasing length (Deegan, 1990; Raynie and Shaw, 1994).

The slower growth rates during the period when feeding structures and feeding strategy begin to change were similar across sampling years and modeling techniques. The growth rates for the pooled model (0.11 mm/day) and yearly two-cycle models (year 1, 0.12 mm/day; year 2, 0.10 mm/day) showed strong agreement with the rates for the age-grouped Laird–Gompertz models (SL grouping: 0.10 mm/day; age grouping: 0.08 mm/day). Although useful in comparisons with previous work, the age-grouped Laird–Gompertz models are less parsimonious and did not capture the ontogenetic shift in feeding strategy from a selective particulate filter feeder to an omnivorous filter feeder, except through

interpretation. The switch of feeding from a selective particulate zooplanktivorous strategy to an omnivorous filter-feeding strategy is likely to drive the lower growth rate during this period (Deegan, 1990; Maillet and Checkley, 1990; Chen et al., 1992; Lozano et al., 2012). Moreover, the decrease in otolith ring width suggested that although daily rings were still accrued, there was limited growth during this time period. Previously reported growth rates of 0.11 mm/day (Raynie, 1991) and 0.12 mm/day (Deegan, 1990) agree with all models in our study. Despite this reduction in growth rate during transformation to the juvenile stage, larval Gulf menhaden may typically undergo another period of rapid growth after 30 mm SL, when the larvae have acquired fully developed feeding structures and are able to filter feed effectively, with growth rates as high as 0.48 mm/day (Deegan, 1990).

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Effects of leader material on catches of shallow pelagic longline fisheries in the southwest Indian Ocean

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Abstract—Catches from a commercial longline fishery targeting swordfish (*Xiphias gladius*) on monofilament nylon leaders were compared with catches on wire leaders in the Indian Ocean. More taxa were caught on wire leaders, which also showed higher catch rates (13% and 56%, in number and weight, respectively) of blue shark (*Prionace glauca*). In contrast, catch rates of swordfish were not significantly affected by leader material. Nylon leaders showed lower at-haulback mortality for most bony fishes, except swordfish. Higher bite-off rates were observed on nylon monofilament, likely owing to the escape of species with sharp teeth, such as sharks. Both leader types caught most species within similar size ranges, but larger mean sizes of blue shark were recorded on wire leaders. The value per unit of effort (VPUE) of the retained catch did not differ between leader materials; however, VPUEs are highly dependent on market fluctuations. Banning wire leaders could be an effective way of reducing shark catches, particularly blue shark catches, in the southwest Indian Ocean.

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Pelagic longlines have historically been used by distant water fleets to catch large tunas (*Thunnus* spp.) and swordfish (*Xiphias gladius*) on the high seas. However, there has been considerable concern over the ecological effects of these fisheries because longline gears also catch other species, particularly billfish (Istiophoridae) and pelagic sharks (Elasmobranchii), and, to a less extent, marine-turtles, sea-birds and marine-mammals (Lewison et al., 2004; Watson and Kerstetter, 2006; Huang, 2011). This range of species is due to the fact that these groups of animals occupy broad geographic ranges spanning geopolitical boundaries and oceanographic regions that support different fisheries (Wallace et al., 2010). Fisheries bycatch—the unintended capture of nontarget organisms during fisheries operations—is therefore a major problem worldwide because it occurs with virtually all fishing fleets and is a global issue for management of marine resources (Hall et al., 2000; Soykan et al., 2008). Despite the existence of extensive differences in bycatch species and the magnitude of these differences from one fishery to another, bycatch can be a driver of declines in marine megafauna populations (Lewison et al., 2004; Read, 2007; Wallace et al., 2010). Such declines can be particularly important in the case of bycatch species that have long life cycles and low productivity, and therefore low potential for population recovery, as is the case for several pelagic sharks.

The large pelagic longline fisheries in the Indian Ocean date back to the 1950s, when the Asian fleets targeted mainly tropical tunas (Lee et al., 2005) and caught billfishes and sharks as bycatch. During the early 1990s, the shallow-setting pelagic longliners (mostly European) expanded the range of their swordfish fishery from the Atlantic Ocean to the Indian Ocean. A few changes were incorporated into the fishing gear in the early 2000s, specifically a shift from traditional to modern gear (Watson and Kerstetter, 2006), making use of mainlines and branch lines of monofilament leader and using lightsticks or flashlights. Moreover, in the same period, the landings of pelagic sharks increased as a result of the increasing interest in the international markets for shark products. Between the mid-2000s and early 2010s, owing to increasing costs (mostly related to the oil prices) and taking advantage of the high

abundance of sharks in particular areas or seasons (or both), the fisheries targeting swordfish started replacing the traditional monofilament leaders with multifilament steel leaders, and baiting the hooks with fish, mostly mackerel (*Scomber* spp.), instead of squid (*Illex* spp.). These gear changes raised concerns about their effects, particularly on shark stocks, because those gear changes were occurring on an ocean-wide scale.

A number of research initiatives have focused on the mitigation of longline bycatch by making several technological and methodological changes, all aiming at increasing the selectivity of fishing gear and reducing mortality. With regard to shark bycatch, particular attention has been given to the use of different hook styles (Watson et al., 2005; Yokota et al., 2006; Coelho et al., 2012a; Amorim et al., 2015) and bait types (Watson et al., 2005; Coelho et al., 2012a; Amorim et al., 2015). However, there are few published studies on the effects of wire leaders on longline catches, despite the general concern regarding increasing catches of sharks. Moreover, a number of these previous studies have reported some contradictory results: Branstetter and Musick (1993) conducted 71 longline sets (using 50 branchlines with nylon leaders and 100 branchlines with wire leaders) and reported higher catch rates of sharks on nylon leaders in inshore waters, but found the opposite in offshore waters; Berkeley and Campos (1988), on the basis of 13 longline sets (about 25% using wire leaders), reported lower catches of sharks on wire leaders than on nylon, but the difference was not statistically significant; Stone and Dixon (2001) completed 10 sets with alternately spaced monofilament and tarred multifilament nylon leaders and reported lower catches for the tarred multifilament nylon leaders; Afonso et al. (2012) completed 17 longline shallow sets, using nylon and wire leaders, and reported higher catches of blue shark (*Prionace glauca*), and all sharks combined on wire leaders; Vega and Licandeo (2009) conducted 37 fishing sets using polyamide monofilament (hooks baited with squid or mackerel) and steel multifilament 3-strand wire (hooks baited with mackerel) and showed marginal differences in shark catch rates, but no differences for the blue shark; and finally, Ward et al. (2008) conducted the largest experiment involving 5 commercial vessels (177 longline sets) targeting tuna (with deep setting), using wire (6 strands) and nylon leaders and reported a higher shark catch rate on wire leaders but did not report any data for the blue shark (the most common species caught on pelagic longlines). Most of these studies were conducted in the northwestern Atlantic Ocean (Branstetter and Musick, 1993; Stone and Dixon, 2001) and the southwestern equatorial regions (Afonso et al., 2012); whereas the remaining studies were conducted in the southwest Pacific Ocean off northeastern Australia (Ward et al., 2008), and in the southeast Pacific Ocean off Easter Island and Salas y Gómez Island (Vega and Licandeo, 2009).

There is a lack of information specific to the Indian Ocean on longlining despite the global landings of sharks on the order of 90,000 metric tons (t) (Indian Ocean Tuna Commission [IOTC] Online Data Querying Service, website). Interestingly, a recent European Union funded research project estimated potential shark catches for the Indian Ocean alone to be on the order of 160,000 t (Murua et al.[1]). In 2015, the Scientific Committee of the IOTC completed its first stock assessment for the blue shark, concluding that the uncertainties in the data and model structure were high, and as such the stock status was uncertain; however, the possibility of the stock being currently overfished was not ruled out (IOTC[2]).

Our study was designed to test the effect of different combinations of the material used on the terminal tackle of the branch lines (monofilament nylon and multifilament wire) on the catches of the shallow pelagic longline fishery targeting swordfish in the southwest Indian Ocean, an area of significant pelagic shark catches. We provide, for the first time for the Indian Ocean and on the basis of a large experimental study, a comparison between the catch composition, catch and yield rates, mortality rates, bite-off rates, and catch-at-size for both target and bycatch species caught by the 2 types of leader materials currently used on pelagic longline fisheries traditionally targeting swordfish.

Materials and methods

Experimental design and data collection

A total of 82 longline sets were carried out during 2 trips in the southwest Indian Ocean, over wide latitudinal (23–32°S) and longitudinal (56–71°E) ranges (Fig. 1) between November 2013 and March 2014. The experiments were conducted by a commercial fishing vessel from the Portuguese pelagic longline fleet. The fishing gear consisted of a standard monofilament polyamide mainline (3.6 mm in diameter), with 6 branch lines between floats (82 m from each other). The branch lines were approximately 18.6 m in length, and were attached to the main line by a 12.5-cm snap. Each branch line had 4 sections: 1) the first section consisted of 2.5-mm nylon monofilament (11.85 m long) connected by a swivel (4.5 cm) to the next section; 2) the second section consisted of a 0.7-m weighed rope (weighing 50 g), connected by a loop to the following section; 3) the third section consisted of 2.2-mm nylon monofilament (5.4 m in length), connected by a loop to the following

[1] Murua, H., F. J. Abascal, J. Amande, J. Ariz, P. Bach, P. Chavance, R. Coelho, M. Korta, F. Poisson, M. N. Santos, et al. 2013. Provision of scientific advice for the purpose of the implementation of the EUPOA sharks. Final report. European Commission Studies for Carrying out the Common Fisheries Policy (MARE/2010/11-LOT 2), 336 p. [Available from website.]

[2] IOTC (Indian Ocean Tuna Commission). 2015. Report of the 18th Session of the IOTC Scientific Committee. Indian Ocean Tuna Commission. Bali, Indonesia, 23–27 November. IOTC-2015-SC18-R[E], 175 p. [Available from website.]

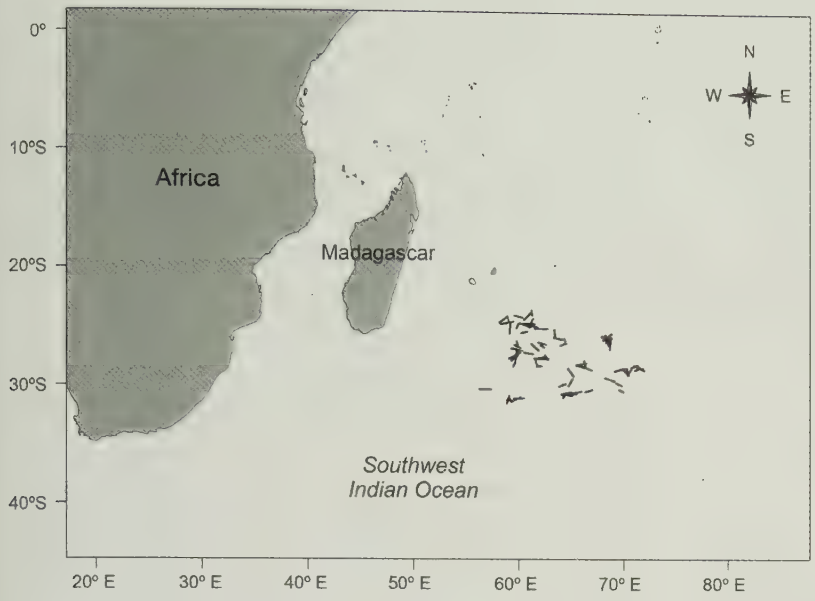

Figure 1

Map of the locations, indicated with black lines, of the experimental longline sets conducted in the southwest Indian Ocean between November 2013 and March 2014 to determine possible effects of leader material on catches of pelagic longline fisheries.

section; in the case of the control; 4) the fourth section consisted of a 2.5-mm nylon monofilament leader (0.65 m in length) with a hook in the terminal tackle, whereas in the case of the treatment (the wire leader), the fourth section consisted of a 1.2-mm multifilament stainless steel leader (3 strands, 0.65 m long) with a hook in the terminal tackle. A battery flashlight (green color) was attached to the loop connecting the second and third sections of the branch lines. Only one hook type was used, specifically a stainless steel 10° offset J hook (model EC-9/0-R[3], Won Yang Fishing Tackle Co. Ltd., Pusan, Korea) that corresponds with the traditional J hook used by the fishery, whose characteristics are summarized in Figure 2. Only one bait type, squid (*Illex* spp.), was used throughout the experiments. Standardized bait was used in all longline sets (squid 24.5 cm [standard deviation (SD) 1.64]). All characteristics of the fishing gear and fishing practices (e.g., gear section placement, setting time, light color, bait size, and hook) were standardized along the 2 trips. The total number of hooks was constant in each set and was the same for each leader type in every set (504 hooks for each leader type material in each set) and fishing occurred at depths of approximately 20–50 m. Gear deployment began traditionally at 1730 h, and haulback started the next day at about 0600 h. Leader type was alternated section by section along the longline, and each section had 84 hooks that were stored in individual "baskets." This alternating of leader types minimized potential confounding effects specific within each set: for example, location, water temperature, fish density, or other factors. Moreover, the branch line type of the first section was changed every set, according to a fixed scheme (i.e., mono:wire:mono:wire, and so on).

Following Watson et al. (2005), we carried out power tests in order to estimate the experimental fishing effort required to detect a fishing method that has different degrees of effectiveness in catching swordfish and blue shark in comparison with the control fishing method. The control fishing method was assumed to be the combination of gear and bait most commonly used in the fishery, specifically J hooks baited with squid, and the power calculations were based on the necessary number of hooks required to detect a 25% and 50% change in the number of swordfish and blue shark caught. A trained observer from the Instituto Português do Mar e da Atmosfera monitored the experimental trials and collected the data on the vessel. Whenever a specimen was caught in the longline, the observer identified the species, recorded the leader line material, the fate (retained or discarded) of a specimen, condition at haulback (alive or dead) and if discarded (alive or dead) and the type of interaction (i.e., hooking location: *mouth* or *jaw*, when the hook was visible; and hooking mode: *deeply ingested*, hook ingested and located in the throat or gut; *externally hooked* when the hook was located externally). The condition of the leaders (bitten-off or not) was recorded. In the case of marine turtles, when possible, they were netted with a large dip net and, whenever possible, the observer and crew attempted to remove fishing gear with long-handled de-hookers and line cutters. The sex of the specimens, both turtles and fish, was determined and size was measured to the nearest lower 1 cm (lower-jaw fork length for billfishes; fork length [FL] for other fishes; carapace curved length for turtles). However, because of the size or weight of some species (i.e., manta rays [*Manta* spp.]) and to increase their survivorship, some specimens were immediately released by cutting off the line.

In the study area, the fleet is currently using mainly monofilament leaders and hooks baited with squid, therefore we considered that the main target species was swordfish. The catch was assigned to 1 of 5 groupings: billfish, which included swordfish and marlins, the latter of which were considered a bycatch; tuna (*Thunnus* spp.), considered bycatch; sharks, which included all elasmobranchs, considered bycatch; other bony fishes, which were assigned exclusively to bycatch species; and turtles. Finally, all the species that were

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

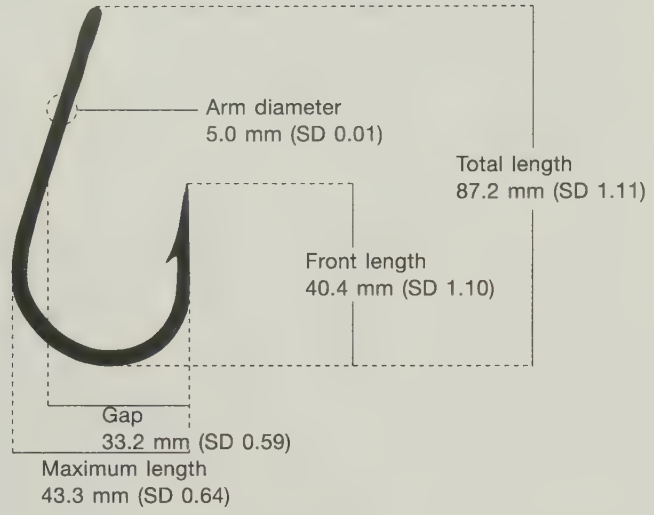

Figure 2

Details of the J hook used in this study on the possible effects of leader material on catches of pelagic longline fisheries in the southwest Indian Ocean. Standard deviations (SDs) are given in parentheses. Hook measurements are shown in the illustration. The offset angle is 10° and refers to the angle of sideways bending of the end of the hook inward in relation to the hook shank.

accidentally caught but not retained were considered discards, consisting mostly of teleost and elasmobranch species with low commercial value or shark species whose retention is currently forbidden by the IOTC, or a combination of both (i.e., bigeye thresher [*Alopias superciliosus*] and oceanic whitetip shark [*Carcharhinus longimanus*]). Other more occasional discards were small specimens of commercial species (e.g., occasional captures of small swordfish) or depredated individuals.

Data analysis

Catch rates were expressed as catch per unit of effort in number of specimens (no. of specimens /1000 hooks ($CPUE_N$). Mortality per unit of effort (MPUE) was also calculated as the number of dead specimens (at haulback) per 1000 hooks (see, for example, Afonso et al., 2012, who used this measure). For the retained species, catch per unit of effort in weight ($CPUE_b$) was also estimated as the weight (in kilograms) per 1000 hooks. Conversion equations were used because the retained catches were processed and frozen onboard and therefore weighing was difficult. For billfishes and tunas, these rates were calculated with the IOTC conversion equations. However, in the case of the remaining species, conversion equations from the Instituto Português do Mar e da Atmosfera (IPMA[4]) were used. The value of the catch per unit of effort (VPUE), measured in euros per 1000 hooks (and given in both U.S. dollars and euros per 1000 hooks), was estimated for the retained species. The reference (price) values used for each species for the VPUE calculations, were those registered for frozen products at the Vigo (Spain) auction in April 2014. The U.S. dollars-to-euro exchange rates were also considered for April 2014. These values were chosen because most European flagged pelagic longliners ship their frozen products to the Vigo market (Amorim et al., 2015).

Kolmogorov–Smirnov tests with Lilliefors correction (Lilliefors, 1969) were used for testing the $CPUE_N$, $CPUE_b$, and MPUE for normality, whereas Levene tests (Levene, 1960) were used for testing the homogeneity of variances. Because of the general lack of normality and homogeneity of variances, the differences between different leader types were tested with randomization tests to determine whether the observed differences between different leader types were significant or whether they were occurring owing to randomness in the sampling (Manly, 2007). For the randomization tests, a Monte Carlo approach was used; the data were randomized and resampled 9999 times to build the expected distribution of the differences under a random distribution and the result was then compared and used to determine the significance of the differences observed in the sample.

For all captured species, the mean length and respective SDs were calculated and for the 2 most abundant species caught (swordfish and blue shark), the size frequency distributions were plotted with histograms. For those 2 species, the mean sizes for the 2 leader types were compared with randomization tests.

The bite-off rates were calculated for each fishing set as the number of missing hooks owing to a cut in the gangion line, per 1000 hooks, within each leader type. The mean and SDs were calculated and plotted, and the differences between leader types were tested with randomization tests.

The relationship between hooking location (mouth or jaw) and hooking mode (deeply ingested, and externally hooked) with leader type material was assessed with plots and with contingency table analysis and chi-square proportion tests. This analysis was performed only for species that numbered >30. In some cases, because of the small sample sizes, particularly for the externally hooked, the analysis was simplified to compare only mouth or jaw and deeply ingested hooking locations.

Generalized linear models with a binomial error distribution and a logit link function were created for determining the influence of changing between the 2 different leader types in the various species or combined taxonomic groups. This was tested both for the catches in number and for the mortalities caused by hooking and was applied only to species or other taxa

[4] IPMA (Instituto Português do Mar e da Atmosfera). 2014. Unpubl. data. Instituto Português do Mar e da Atmosfera, Rua C do Aeroporto, 1749-077 Lisboa, Portugal.

for catches with greater than 30 individuals. The response variable of the models was the proportion of the catches (or dead specimens in the mortality models) in each longline set, calculated as the number of animals (or dead specimens in the mortality models) given the number of hooks used in each set. The odds-ratios of the parameters with their respective 95% confidence intervals (CIs) were calculated and used for interpretation. For this purpose, the monofilament leader was considered the baseline (control) configuration, and the odds-ratios were calculated for changing to the alternative wire (experimental) leader.

Data analysis for this study was carried out with R statistical software, vers. 3.2.0 (R Core Team, 2015). Most analyses were performed with functions available in the core R program. Additional libraries were used for the Levene tests to compare homogeneity of variances (library car; Fox and Weisberg, 2011) and for the permutation tests (library perm; Fay and Shaw, 2010). Plots were built by using ggplot2 (Wickham, 2009), and the map was built by using mapplots (Gerritsen, 2014), shapefiles (Stabler, 2013), and a function for the north arrow created by Tanimura et al. (2007).

Results

Power tests

Overall, a total of 82,656 hooks were used during the experimental fishing sets (82 sets), corresponding to 41,328 hooks of each leader type. According to the conducted power analysis, the number of hooks deployed is larger than that necessary to detect a 50% (5904 hooks) or 25% (23,613 hooks) change in the catch rates (in number) of the blue shark, the most captured shark species in Indian Ocean pelagic longline fisheries. The same was also true for detecting such a change in swordfish catch rates (5088 and 20,346 hooks, respectively).

Catch composition

A total of 33 taxa were caught during this study, specifically 11 species of sharks (2 species belonging to Mobulidae), 6 species of billfish, 3 species of tuna, 12 species of other bony fishes and a single species of marine turtle (Table 1). For the species composition of the catch, the highest number of species was recorded for wire leaders (31 out of the 32), compared with 24 taxa caught with monofilament leaders. For the different groups of species, monofilament leaders in contrast to wire leaders resulted in the catch of an equal number of billfish and tuna species, but a lower number of sharks (7 *vs.* 9) and other bony fishes (8 *vs.* 12, respectively)

A total of 2385 specimens were caught during this study, of which 329 were discarded either because they were noncommercial species, belonged to species whose retention is prohibited by the IOTC, or they were damaged by depredation. Among the overall catch there were 1077 billfishes, 845 sharks, 412 other bony fishes, 50 tuna, and a single marine turtle, as summarized in Table 1. A total of 15 taxa were retained in the experiments, the swordfish and blue shark being the most abundant species, representing 50.1% and 37.3% of the retained catches in number, respectively. All the remaining species represented less than 1.5% of the total retained catch in number, the exceptions being 2 other bony species, the dolphinfish (*Coryphaena hippurus*) and the escolar (*Lepidocybium flavobrunneum*), which represented 6.7% and 3.0%, respectively (Table 1). In addition, 18 taxa were systematically discarded, specifically 9 sharks, 8 other bony fishes and a marine turtle, the loggerhead turtle (*Caretta caretta*). Amongst the discarded groups of species, other bony fishes and sharks accounted for 64.7% and 15.8% of the discarded specimens, whereas commercial species such as billfishes (10.3%) and tunas (0.9%) were also discarded owing to predation or the small size of specimens. The most commonly discarded bony fishes were the longnose lancetfish (*Alepisaurus ferox*) and snake mackerel (*Gempylus serpens*), accounting for 28.6% and 26.7% of discards, respectively. In the case of elasmobranchs, the pelagic stingray (*Pteroplatytrygon violacea*) was the most commonly discarded species (7.6%), followed by the 2 shark species prohibited to be fished: the bigeye thresher (3.0%) and the oceanic whitetip shark (2.4%). The frequency of occurrence varied greatly among species, with the swordfish being the most frequently caught species (present in 100% of the sets), followed by the blue shark (91.5%), dolphinfish (37.8%), longnose lancetfish (36.6%), and snake mackerel (29.3%) (see details in Table 1).

Catch rates

The effects of the leader type on the $CPUE_N$ were group and taxon specific. The values of $CPUE_N$ were higher when wire leaders were used for other bony fishes and sharks, as well as for the overall catch (on average 32%, 30% and 13%, with 95% CIs of 8–60%, 13–49% and 5–23%, respectively). At the species level, only $CPUE_N$ for blue sharks showed a significant increase on wire leaders, which was on the order of 31%, with 95% CIs varying between 14% and 52% (Fig. 3). Swordfish and billfishes showed lower $CPUE_N$ on wire leaders, but the detected differences were not significant. The effects of the leader type on the $CPUE_b$ of retained species were again group and taxon specific. However, in the $CPUE_b$, higher catch rates on wire were noted only for the shark group, blue shark in particular and the overall retained catch (on average 53%, 56% and 15%, respectively). In the case of the target species (swordfish), although the wire leaders had a negative effect (decrease of 11%) on the mean $CPUE_b$, this effect was not statistically significant (Tables 1 and 2).

In terms of the VPUE, no significant differences were detected in changes from monofilament to wire leaders (permutation test: difference in means= –$44.99 (–€32.62), P=0.874) because the decrease of swordfish

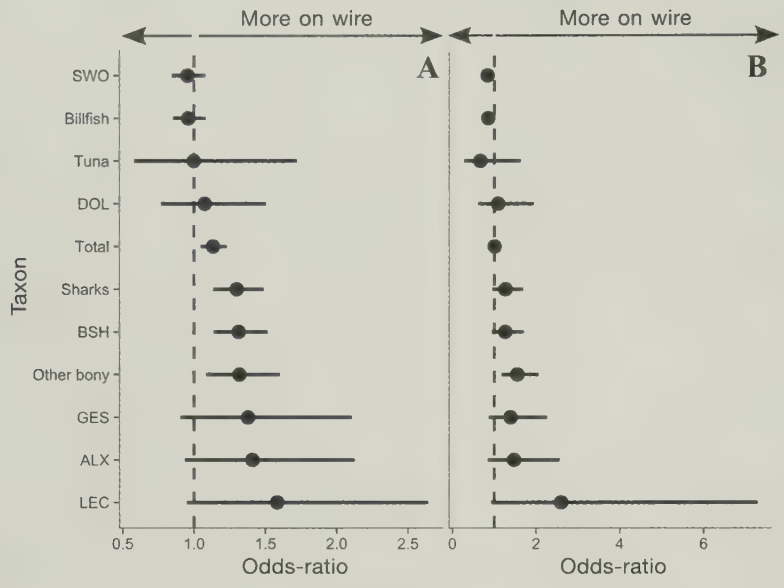

Figure 3

Odds-ratios of the (**A**) catch rates in number and (**B**) hooking mortality for the change from the leader material from monofilament to wire for species and species groups caught during longline sets conducted during November 2013–March 2014 in the southwest Indian Ocean. Food and Agriculture Organization of the United Nations species codes are used: SWO=swordfish (*Xiphias gladius*); DOL=dolphinfish (*Coryphaena hippurus*); BSH=blue shark (*Prionace glauca*); GES=snake mackerel (*Gempylus serpens*); ALX=longnose lancetfish (*Alepisaurus ferox*); and LEC=escolar (*Lepidocybium flavobrunneum*). The models and odds-ratios were calculated only for species or combined taxa with 30 or more individuals. The error bars indicate the 95% confidence intervals of the odds-ratios. The vertical dashed line indicates the reference of the odds-ratios (1=no change). The top arrow represents the increase in the odds-ratios when changing from 2.5-mm monofilament nylon to 1.2-mm multifilament stainless wire leaders.

catch rates was compensated by the increase of blue shark retention (Table 1).

The mean bite-off rates for wire and monofilament leaders were 1.38/1000 hooks and 5.37/1000 hooks, respectively. These differences were found to be significant (permutation test: difference in means=3.99, $P<0.001$). Regarding hooking location, most shark species were deeply hooked (58% overall, 60% for the blue shark and 50% for the shortfin mako (*Isurus oxyrinchus*), respectively). The pelagic stingray was an exception, where specimens were mostly hooked by the mouth or jaw (83%). In contrast, most tunas and billfish species were retained, having been hooked in the mouth, except for the swordfish, which was predominantly deeply hooked (85%, and 12% and 2% were retained, having been hooked in the mouth and externally, respectively). No differences were detected when comparing hooking location between the 2 different types of leader material, for the main species, the swordfish (contingency table analysis: $P>0.05$ for all cases; Fig. 4)

Mortality rates

The effects of the leader type in terms of mortality rates (in number) at haulback varied among the different species groups and taxa. The mortality models detected significantly less mortality from hooking for the swordfish when wire leaders were used, showing a 16% decrease in the mortalities (95% CI varying between 2% and 28%) and also for the billfishes group with a 15% decrease in the mortalities (95% CI varying between 1% and 26%). In contrast, for the other bony fishes there was an increase in hooking mortality of 55% when wire leaders were used (95% CI varying between 17% and 100%). For the blue shark the hooking mortality also increased when wire leaders were used (26% in the point estimate) but this increase was not statistically significant because the 95% CIs varied between a decrease of 6.5% and an increase of 71% with the use of wire. The same was observed for the shark group combined; the point estimate showed a decrease in hooking mortality of 27% when wire leaders were used, but the 95% CI varied between a decrease of 5% and an increase of 70%, indicating that the effects were not statistically significant (Tables 1 and 2, Fig. 3).

Size distribution of retained species

Statistics of the size structure of the species caught on the different leader materials tested during this study are summarized in Table 3. For most species caught, there were no major differences in size range and mean size for the different leader types tested (Table 3). However, for the blue shark, a wider size range was recorded and significant differences in the mean size were detected, and slightly larger sizes were captured with wire leaders (mean size: 198.2 cm FL [SD 38.15] vs. than with monofilament leaders (mean size 190.6 cm FL [SD 35.32]). For swordfish, very similar size ranges were observed and no significant differences were detected in the mean size captured for the 2 leader materials (Fig. 5, Table 3).

Discussion

The results from this study show that leader material had an effect on the catch composition of a longline fishery and that wire leaders caught more species. This result contrasts with those reported by Ward et al.

Table 1

Means and standard deviations (SDs) for catch in number ($CPUE_N$) and weight ($CPUE_b$) per unit of effort (per 1000 hooks), mortality (MPUE) per unit of effort (1000 hooks) by species and species groups caught by using 2 different leader materials, 2.5-mm monofilament nylon and 1.2-mm multifilament stainless wire, during experimental longline sets conducted in the southwest Indian Ocean between November 2013 and March 2014. Other values given are number of specimens caught (no.); frequency of occurrence (FO), measured as a percentage; discards (Disc), measured as a percentage; dead discards (DD), measured as a percentage; and the value per unit of effort (per 1000 hooks) of the retained catch (VPUE), given in U.S. dollars ($) and euros (€).

		Monofilament									Wire								
Group and Species	No.	FO	Disc	DD	$CPUE_N$	SD	MPUE	SD	$CPUE_b$	SD	FO	Disc	DD	$CPUE_N$	SD	MPUE	SD	$CPUE_b$	SD
Billfish																			
Istiompax indica	2	1.2	0.0	0.0	0.0	0.2	0.0	0.2	2.7	24.8	1.2	0.0	0.0	0.0	0.2	0.0	0.0	3.0	27.6
Makaira nigricans	7	4.9	0.0	0.0	0.1	0.4	0.0	0.2	16.8	75.2	3.7	0.0	0.0	0.1	0.4	0.0	0.3	9.9	51.5
Kajikia audax	22	12.2	7.7	7.7	0.3	1.0	0.2	0.7	10.6	31.0	9.8	22.2	22.2	0.2	0.7	0.1	0.4	5.8	21.9
Istiophorus platypterus	7	2.4	0.0	0.0	0.0	0.3	0.0	0.0	2.1	13.7	6.1	0.0	0.0	0.1	0.5	0.1	0.4	5.0	20.2
Tetrapturus angustirostris	8	2.4	0.0	0.0	0.0	0.3	0.0	0.2	6.9	44.0	7.3	16.7	16.7	0.1	0.5	0.1	0.5	15.8	63.2
Xiphias gladius	1031	100.0	2.7	1.9	12.8	6.1	9.1	5.3	648.5	357.6	98.8	3.2	3.0	12.2	6.2	7.7	4.2	583.2	348.5
Total billfish	1077				13.3	6.2	9.4	5.3	687.6	372.2	–	–	–	12.8	6.4	8.0	4.4	622.8	373.9
Tuna																			
Thunnus alalunga	9	6.1	0.0	0.0	0.2	0.8	0.1	0.4	4.0	18.4	2.4	0.0	0.0	0.1	0.4	0.0	0.2	1.5	7.6
Thunnus obesus	22	8.5	14.3	14.3	0.2	0.6	0.1	0.4	6.7	29.9	15.9	6.7	6.7	0.4	0.9	0.1	0.5	15.6	42.2
Thunnus albacares	19	12.2	9.1	9.1	0.3	0.7	0.1	0.4	13.1	44.9	8.5	0.0	0.0	0.2	0.7	0.0	0.4	12.5	43.5
Total tuna	50				0.6	1.3	0.3	0.8	23.9	61.9	–	–	–	0.6	1.2	0.2	0.7	29.5	66.8
Other bony fishes																			
Alepisaurus brevirostris	6	3.7	100.0	33.3	0.1	0.4	0.0	0.2	–	–	3.7	100.0	100.0	0.1	0.4	0.1	0.4	–	–
Alepisaurus ferox	94	36.6	100.0	64.1	0.9	1.4	0.5	1.0	–	–	46.3	100.0	61.8	1.3	1.8	0.8	1.5	–	–
Sphyraena spp.	5	–	–	–	–	–	–	–	–	–	4.9	100.0	100.0	0.1	0.6	0.1	0.4	–	–
Centrolophidae	1	–	–	–	–	–	–	–	–	–	1.2	100.0	100.0	0.0	0.2	0.0	0.2	–	–
Coryphaena hippurus	137	37.8	4.5	4.5	1.6	2.9	0.5	1.4	12.5	24.4	39.0	9.9	9.9	1.7	3.1	0.6	1.5	10.9	21.2
Gempylus serpens	88	29.3	100.0	89.2	0.9	1.7	0.7	1.4	–	–	39.0	100.0	82.4	1.2	2.2	0.9	2.0	–	–
Lampris guttatus	1	–	–	–	–	–	–	–	–	–	1.2	100.0	100.0	0.0	0.2	0.0	0.2	–	–
Lepidocybium flavobrunneum	62	20.7	0.0	0.0	0.6	1.3	0.1	0.5	7.3	18.9	36.6	10.5	7.9	0.9	1.4	0.3	0.7	9.5	17.6
Mola spp.	3	2.4	100.0	0.0	0.0	0.3	0.0	0.0	–	–	1.2	100.0	0.0	0.0	0.2	0.0	0.0	–	–
Ruvettus pretiosus	6	4.9	50.0	25.0	0.1	0.4	0.0	0.0	0.1	0.4	2.4	100.0	100.0	0.0	0.3	0.0	0.2	–	–
Regalecidae	1	–	–	–	–	–	–	–	–	–	1.2	100.0	100.0	0.0	0.2	0.0	0.0	–	–
Acanthocybium solandri	7	2.4	50.0	50.0	0.0	0.3	0.0	0.2	0.2	2.0	6.1	40.0	40.0	0.1	0.5	0.1	0.4	0.4	2.1
Total other bony fishes	412	–	–	–	4.3	3.6	1.9	2.5	20.1	28.6	–	–	–	5.7	4.8	2.9	3.6	20.7	26.6
Sharks																			
Prionace glauca	767	91.5	4.2	0.3	8.0	6.3	1.8	2.7	416.6	305.9	96.3	0.5	0.2	10.5	7.9	2.3	3.0	650.1	474.4
Alopias superciliosus	10	8.5	100.0	55.6	0.2	0.8	0.1	0.5	–	–	1.2	100.0	100.0	0.0	0.2	0.0	0.2	–	–
Manta sp.	1	–	–	–	–	–	–	–	–	–	1.2	100.0	0.0	0.0	0.2	0.0	0.0	–	–
Carcharhinus longimanus	8	1.2	100.0	0.0	0.0	0.2	0.0	0.0	–	–	8.5	100.0	28.6	0.2	0.6	0.0	0.3	–	–
Pteroplatytrygon violacea	25	11.0	100.0	0.0	0.3	0.9	0.0	0.0	–	–	14.6	100.0	0.0	0.3	0.8	0.0	0.0	–	–
Lamna nasus	2	–	–	–	–	–	–	–	–	–	2.4	100.0	0.0	0.0	0.3	0.0	0.0	–	–
Pseudocarcharias kamoharai	1	–	–	–	–	–	–	–	–	–	1.2	100.0	0.0	0.0	0.2	0.0	0.0	–	–
Mobula sp.	1	1.2	16.7	0.0	0.0	0.2	0.0	0.0	–	–	–	–	–	–	–	–	–	–	–
Isurus oxyrinchus	26	14.6	16.7	0.0	0.3	0.7	0.0	0.2	23.6	66.5	15.9	0.0	0.0	0.3	0.8	0.0	0.3	25.4	68.5
Sphyrna sp.	1	1.2	100.0	0.0	0.0	0.2	0.0	0.0	–	–	–	–	–	–	–	–	–	–	–
Sphyrna zygaena	3	–	–	–	–	–	–	–	–	–	3.7	100.0	100.0	0.1	0.4	0.1	0.4	–	–
Total sharks	845	–	–	–	8.9	6.5	2.0	2.8	440.1	323.3	–	–	–	11.5	8.0	2.5	3.3	675.5	475.6
Turtles																			
Caretta caretta	1	–	–	–	–	–	–	–	–	–	1.2	100.0	0.0	0.0	0.2	0.0	0.0	–	–
Total turtles	1	–	–	–	–	–	–	–	–	–		–	–	0.0	0.2	0.0	0.0	–	–
Total overall	2385	–	–	–	27.1	9.6	13.6	6.5	1167.7	525.9	–	–	–	30.6	10.8	13.7	6.7	1347.1	588.7
VPUE of retained catch					$3869.9 (SD 1870.3) (€2805.5 [SD 1355.9])									$3902.9 (SD 1803.2) (€2829.4 [SD 1307.2])					

Table 2

Results of the permutation (perm) tests for statistical comparison between catch in number ($CPUE_N$) and weight ($CPUE_b$) per unit of effort (per 1000 hooks) and mortality (MPUE) per unit of effort (per 1000 hooks) by species and species groups caught by 2 different leader materials, 2.5-mm monofilament nylon and 1.2-mm multifilament stainless wire, during experimental longline sets conducted in the southwest Indian Ocean between November 2013 and March 2014.

	$CPUE_N$		MPUE		$CPUE_b$	
Group and species	Perm test	*P*	Perm test	*P*	Perm test	*P*
Billfish						
Istiompax indica	0.00	1.00	0.02	1.00	−0.31	1.00
Makaira nigricans	0.02	1.00	−0.02	0.99	6.87	0.48
Kajikia audax	0.10	0.58	0.10	0.46	4.85	0.24
Istiophorus platypterus	−0.07	0.44	−0.10	0.12	−2.88	0.32
Tetrapturus angustirostris	−0.10	0.29	−0.10	0.22	−8.94	0.36
Xiphias gladius	0.56	0.57	1.45	0.05	65.26	0.24
Total billfish	0.51	0.62	1.36	0.08	64.85	0.27
Tuna						
Thunnus alalunga	0.12	0.35	0.07	0.37	2.57	0.25
Thunnus obesus	−0.19	0.15	−0.02	1.00	−8.90	0.13
Thunnus albacares	0.07	0.66	0.05	0.73	0.69	0.90
Total tuna	0.00	1.00	0.10	0.51	−5.64	0.59
Other bony fishes						
Alepisaurus brevirostris	0.00	1.00	−0.05	0.62	–	–
Alepisaurus ferox	−0.39	0.13	−0.24	0.27	–	–
Sphyraena spp	−0.12	0.12	−0.10	0.12	–	–
Centrolophidae	−0.02	1.00	−0.02	1.00	–	–
Coryphaena hippurus	−0.12	0.79	−0.05	0.86	1.60	0.65
Gempylus serpens	−0.34	0.30	−0.27	0.35	–	–
Lampris guttatus	−0.02	0.99	−0.02	0.99	–	–
Lepidocybium flavobrunneum	−0.34	0.15	−0.19	0.08	−2.18	0.45
Mola spp.	0.02	1.00	–	–	–	–
Ruvettus pretiosus	0.05	0.68	−0.02	1.00	–	–
Regalecidae	−0.02	1.00	–	–	–	–
Acanthocybium solandri	−0.07	0.44	−0.07	0.36	−0.14	0.75
Total other bony fishes	−1.36	0.04	−1.04	0.03	−0.65	0.88
Sharks						
Prionace glauca	−2.49	0.03	−0.48	0.28	−233.52	0.00
Alopias superciliosus	0.19	0.05	0.10	0.21	–	–
Manta sp.	−0.02	0.99	–	–	–	–
Carcharhinus longimanus	−0.15	0.07	−0.05	0.50	–	–
Pteroplatytrygon violacea	−0.02	1.00	–	–	–	–
Lamna nasus	−0.05	0.51	–	–	–	–
Pseudocarcharias kamoharai	−0.02	1.00	–	–	–	–
Mobula sp.	0.02	0.99	–	–	–	–
Isurus oxyrinchus	−0.05	0.82	−0.02	1.00	−1.84	0.85
Sphyrna sp.	0.02	1.00	–	–	–	–
Sphyrna zygaena	−0.07	0.23	−0.07	0.23	–	–
Total sharks	−2.64	0.02	−0.53	0.27	−235.37	0.00
Turtles						
Caretta caretta	−0.02	0.99	–	–	–	–
Total turtles	−0.02	0.99	–	–	–	–
Total overall	−3.53	0.03	−0.12	0.92	−179.38	0.04

(2008), who found the same number of species caught with both leader types, and those observed by Vega and Licandeo (2009), who found that monofilament gear caught more species. Theoretically, monofilament nylon leaders may be more difficult than wire leaders of the same diameter to be visually detected, but are also more easily severed than wire leaders. One possible reason for the different results may be related to differences in availability of species in the study areas, as well as their relative ability to bite through a leader. However, it should also be noted that other gear characteristics, such as hook style and size can also influ-

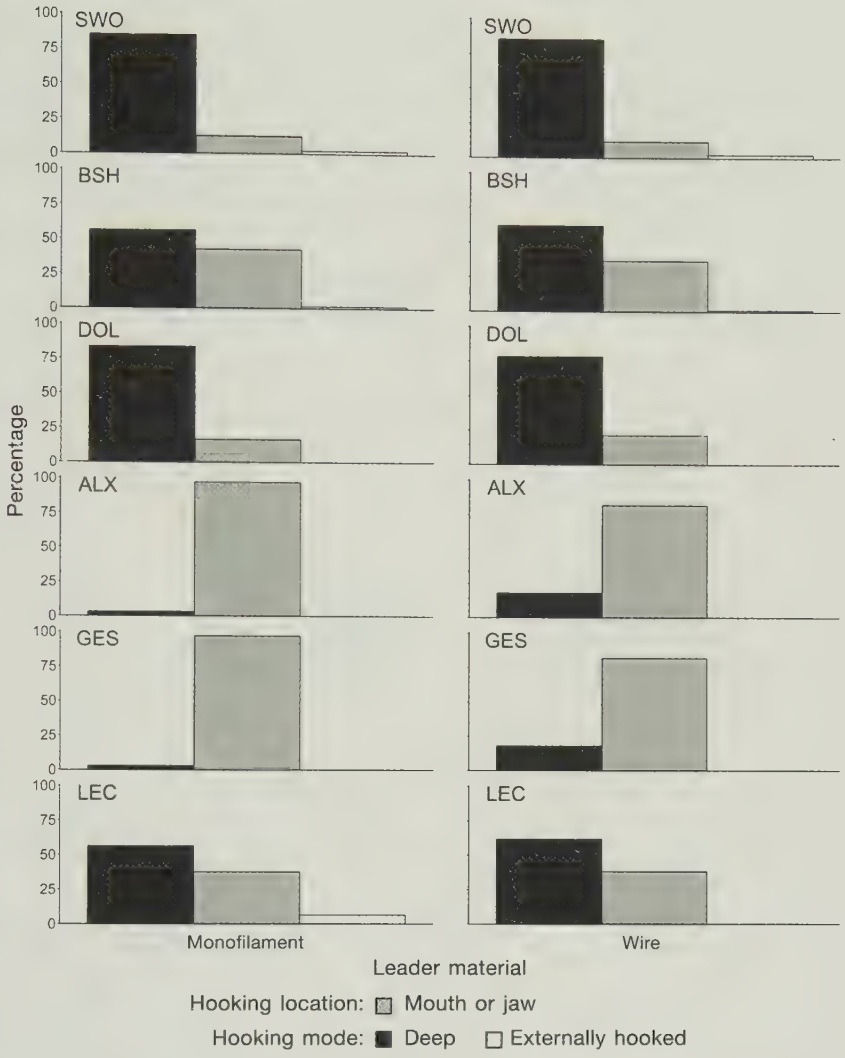

Figure 4

Hooking location by leader material for the main species (no. >30) captured in 2013–2014 in the southwest Indian Ocean. Food and Agriculture Organization of the United Nations species codes are used: SWO=swordfish (*Xiphias gladius*); BSH=blue shark (*Prionace glauca*); DOL=dolphinfish (*Coryphaena hippurus*); ALX=longnose lancetfish (*Alepisaurus ferox*); GES=snake mackerel (*Gempylus serpens*); and LEC=escolar (*Lepidocybium flavobrunneum*). The bars refer to the percentage of each hooking location for each leader material: 2.5-mm monofilament nylon and 1.2-mm multifilament stainless wire.

ence the catch and could contribute to the differences between studies. Specifically, Vega and Licandeo (2009) used J hooks similar to those used in our study and as such the results are more directly comparable, whereas Ward et al. (2008) used Japanese tuna hooks with 10° offset. Another factor causing differing results may be related to the bait. Vega and Licandeo (2009) used a mix of squid and mackerel as bait on sets with nylon leaders and just mackerel on sets with wire leaders, whereas we used squid bait exclusively, which is the most commonly used bait in this fishery for targeting swordfish. Finally, it should also be noted that there was a difference in effort in terms of the number of sets conducted in each study, specifically 82 sets in our study, 37 sets in Vega and Licandeo (2009) and 177 sets in Ward et al. (2008).

Leader type also had a significant effect in terms of relative catchability in both number and weight for some of the species or species groups (or combination of both) in this pelagic longline fishery. The use of monofilament leaders trended toward higher catch rates of swordfish (although not statistically significant) and

Table 3

Statistics of the size structure of the species caught during longline sets conducted in the southwest Indian Ocean between November 2013 and March 2014 and results of the permutation (perm) tests for statistical comparison of mean sizes (in cm) for the 2 leader materials tested, 2.5-mm monofilament nylon and 1.2-mm multifilament stainless wire. Also provided are the number of specimens measured (no.) as well as the range and mean, with standard deviation (SD), of the sizes in the catch for each species or species group. Size measurements refer to the length (in centimeters): lower-jaw fork length for billfishes, fork length for all other fishes, and total carapace curve length for marine turtles.

	Monofilament				Wire					
Group and species	No.	Range	Mean	SD	No.	Range	Mean	SD	Perm test	*P*
Billfish										
Istiompax indica	1	227–227	227.0	0.0	1	235–235	235.0	0.0	–	–
Makaira nigricans	4	245–277	264.5	13.9	3	236–258	245.7	11.2	18.83	0.11
Kajikia audax	13	175–228	194.2	18.4	8	175–217	192.3	13.9	1.90	0.83
Istiophorus platypterus	2	210–211	210.5	0.7	5	184–219	205.6	13.4	–	–
Tetrapturus angustirostris	2	155–165	160.0	7.1	6	146–163	155.3	7.2	–	–
Xiphias gladius	519	64–249	151.9	30.6	499	67–251	149.9	29.3	2.00	0.28
Tuna										
Thunnus alalunga	7	98–109	103.3	3.7	3	98–102	100.0	2.0	3.29	0.25
Thunnus obesus	6	76–162	121.3	38.2	14	76–164	127.2	22.9	–5.88	0.67
Thunnus albacares	11	80–165	137.8	22.6	8	132–172	148.5	15.7	–10.68	0.29
Other bony fishes										
Alepisaurus brevirostris	3	68–92	77.3	12.9	3	64–100	81.3	18.0	–4.00	0.78
Alepisaurus ferox	37	71–139	102.3	18.2	54	45–152	102.5	23.5	–0.24	0.97
Sphyraena spp	–	–	–	–	4	94–132	118.8	17.7	–	–
Centrolophidae	–	–	–	–	1	76–76	76.0	0.0	–	–
Coryphaena hippurus	66	67–130	101.7	13.5	71	65–121	96.9	12.4	4.77	0.03
Gempylus serpens	37	78–155	105.9	15.0	51	77–149	107.6	14.1	–1.78	0.58
Lampris guttatus	–	–	–	–	1	106–106	106.0	0.0	–	–
Lepidocybium flavobrunneum	24	64–132	104.1	17.5	36	51–136	97.6	21.7	6.49	0.23
Ruvettus pretiosus	4	49–60	55.5	4.8	2	54–55	54.5	0.7	–	–
Regalecidae	–	–	–	–	1	171–1	171.0	0.0	–	–
Acanthocybium solandri	1	141–141	141.0	0.0	5	100–140	119.2	17.3	–	–
Sharks										
Prionace glauca	318	127–281	190.6	35.3	433	108–279	198.2	38.1	–7.64	0.00
Alopias superciliosus	5	115–192	171.0	31.6	1	162–162	162.0	0.0	–	–
Carcharhinus longimanus	–	–	–	–	3	88–148	108.3	34.4	–	–
Lamna nasus	–	–	–	–	1	247–247	247.0	0.0	–	–
Pseudocarcharias kamoharai	–	–	–	–	1	88–88	88.0	0.0	–	–
Isurus oxyrinchus	10	152–228	204.3	23.1	14	138–227	186.4	26.9	17.87	0.10
Sphyrna zygaena	–	–	–	–	3	169–179	173.3	5.1	–	–
Turtles										
Caretta caretta	–	–	–	–	1	65–65	65.0	0.00	–	–

lower catch rates of sharks, particularly blue shark. Other authors have reported similar results in the Atlantic (Afonso et al., 2012) and Pacific oceans (Ward et al., 2008; Vega and Licandeo, 2009). However, earlier studies in the Atlantic Ocean, by Branstetter and Musick (1993) and Stone and Dixon (2001), showed the opposite result for the blue shark. Differences in the length of wire leaders, diameter of monofilament leaders and target species may account for the differences in catches rates among studies. For example, in the Stone and Dixon (2001) study the lower section (leader) of both gangion types was monofilament nylon and the upper section varied between tarred and no-tarred nylon material. Additionally, in our study the wire leaders were 2 to 3 times longer than those used in earlier studies and this change could have contributed to some of the observed differences.

As with our study, other authors have also reported similar trends in rates of bite-offs and that most of these events occurred when the use of nylon leaders (e.g., Ward et al., 2008; Afonso et al., 2012). However, the level of bite-off rates varies considerably between the fishing grounds and fisheries. We found rates similar to those reported by Afonso et al. (2012) for a Brazilian swordfish fishery in the Atlantic Ocean (about 30% of shark catches), but much lower rates (by one order of magnitude) than those reported by observers on a tuna longline off northeastern Australia (Ward et al., 2008). Among the captured species, sharks are most likely to be responsible for the majority of bite-

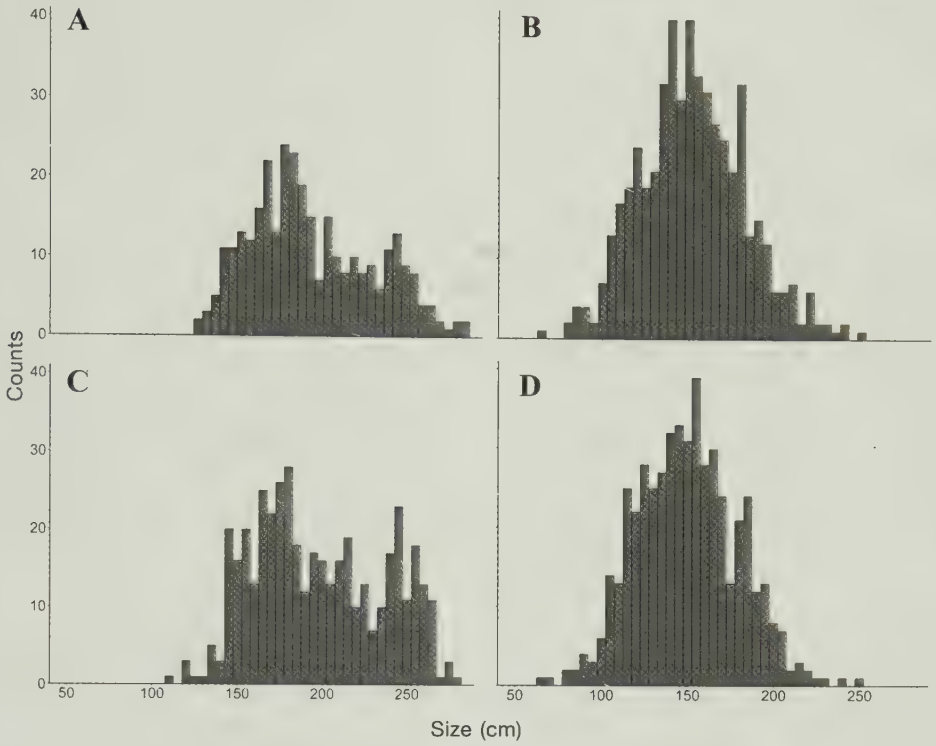

Figure 5

Size distributions for the 2 major species caught during 2013–2014 in the southwest Indian Ocean. (**A**) blue shark (*Prionace glauca*) caught with 2.5-mm monofilament nylon; (**B**) swordfish (*Xiphias gladius*) caught with 2.5-mm monofilament nylon; (**C**) blue shark (*Prionace glauca*) caught with 1.2-mm multifilament stainless wire; (**D**) swordfish (*Xiphias gladius*) caught with 1.2-mm multifilament stainless wire. Size measurements are given in centimeters: lower-jaw fork length for swordfish and fork length for blue shark.

offs because these bite-offs were more frequent on sets with the highest shark catch rates. Moreover, several shark bite-offs were observed during the fishing experiments by the fishery observers. However, other species that also have sharp teeth, such as the snake mackerel or the dolphinfish, could also escape the longline by severing the leaders. Other important aspects related to bite-off rates are the hook styles used and hooking location. Circle hooks primarily embed in the corner of the jaw (Prince et al., 2002; Skomal et al., 2002) and J hooks are more likely to be swallowed, causing deep hooking in the throat or gut. Deep hooking, which was the most common retention mode recorded in our study with the J hook, can result in leaders becoming more exposed to abrasion against teeth.

Very few authors have discussed the effects of gear material on mortality at haulback. As in our study, Afonso et al. (2012) also did not find significant differences when comparing shark MPUE between leader types, although the mortalities were slightly higher when using wire leaders. On the other hand, we recorded higher swordfish MPUE on wire. We cannot explain such a result, particularly as the mean $CPUE_N$ and $CPUE_b$ were similar for both leader materials. In addition, the size selectivity of gear material has been poorly studied. Although it would appear that leader material has no effect on size selectivity for most species, in the case of blue shark, a wider size range and a larger mean size were observed with the use of wire leaders, which reinforces the previously reported observation (Afonso et al., 2012) that wire leaders retain the more resilient and larger blue shark specimens.

Although a relatively small number of specimens of other shark species were caught during our experiment, the dead *versus* alive ratios (mortality at haulback) observed were consistent with those reported by Coelho et al. (2012b) for a similar fishery in the Atlantic Ocean. The exception was the shortfin mako, which in this case showed a much lower mortality ratio at haulback (7–15%). Coelho et al (2012b) reported a relationship between hooking mortality and specimen size for the shortfin mako in the Atlantic Ocean, with larger specimens having a lower probability of being dead at haulback. Because the size distribution in this region of the Indian Ocean tends to be composed of larger specimens than those in the Atlantic Ocean, as report-

ed by the Coelho et al. (2012b) study (Atlantic Ocean: mean size=168.8 cm FL [SD 35.4], range=66–305 cm FL; Indian Ocean: mean size=193.9 cm FL [SD 24.6], range=138–228 cm FL), such differences could be a reason for the lower hooking mortality of the shortfin mako in the Indian Ocean.

According to our results, there was not a significant difference in the VPUE, but it should be noted that our estimates were based on the average market price for a single month. A range of prices would, perhaps, better reflect market fluctuations. On the other hand, current perceptions of fishermen are that changing the bait from the more expensive squid to cheaper mackerel, is worthwhile in areas or seasons of high shark abundance (representing over 50% of the retained catch), as reported by Amorim et al. (2015) in a similar fishery in the southern Atlantic Ocean. Therefore, a thorough assessment (including the cost of replacing and repairing damaged gear) of the economic impact of banning wire leaders will be required if fisheries managers wish to consider such a measure to reduce unwanted bycatch in longline fisheries.

The interaction of bycatch species with longlining gear raises a number of other concerns, namely their postrelease mortality (Gilman et al., 2008). Moyes et al. (2006), using a scientific crew, investigated postrelease survival of blue shark in longline fisheries in the Pacific Ocean, whereas Campana et al. (2009) conducted a similar experiment in the Atlantic Ocean but on commercial vessels. These authors used pop-up satellite archival tags that recorded postrelease survival rates of blue shark of 100% (Moyes et al.) and 81%, (Campana et al.); the differences were attributed to the different study design, gear configuration (e.g., hook style and size, quantity of hooks and soaking time) and handling practices by the scientific crew in Moyes et al. (2006). It is known that the blue shark is a hardy shark species, and individuals are often recovered with one or more hooks in their bodies or mouth from previous captures (senior author, personal observ.). However, it is not common to find reports of protected shark species or small sharks (or both), or commonly discarded bony fishes, with hooks embedded in their jaws from past interactions with longline gear. Therefore, we may assume that postrelease mortality rates are likely higher for those species. Campana et al. (2015) showed that porbeagles (*Lamna nasus*) and shortfin makos experienced much greater mortality than blue sharks in the Canadian pelagic longline fishery, and about one-half of the hooked porbeagles and shortfin makos died during or after fishing owing to hooking or postrelease mortality. Additionally, we should note that Campana et al. (2015) used mainly circle hooks, whereas in our study we used J hooks that can affect the hooking location (mouth or jaw *vs.* deeply hooked) and consequently on the injuries of the discarded specimens. Apart from high mortality at haulback for many shark species (Coelho et al., 2012b), we also found high mortality rates at haulback with the use of nylon monofilament and wire leaders for commonly discarded species such as the longnose lancetfish (60% and 61%), and the snake mackerel (88% and 81%, respectively),

The results of our work support banning wire leaders as an effective way of reducing shark bycatch in general, of lowering the number of sharks landed and, consequently, is an effective way of decreasing shark mortality in a fishery where the blue shark and the shortfin mako are currently the only shark species retained. At least some sharks are able to escape and survive by severing the nylon leaders, although their fate (delayed mortality) is still poorly known. The introduction of wire leaders in the southwest Indian Ocean swordfish longline fishery was a consequence of lower catch rates of the target species and a response to the increase in exploitation costs, with the objective of increasing the revenues of fishermen. Fishery managers considering the banning of wire leaders in this swordfish fishery need to balance the potential beneficial effects on shark populations (particularly blue shark and shortfin mako) with the potential adverse effects on other species (particularly swordfish, as catches could increase). A reduction in the current catch levels of sharks should have a positive impact on the stocks, even though the current status of the shark stocks is unknown. According to the IOTC[2], in the case of blue sharks, maintaining or increasing fishing effort will result in further declines in biomass, productivity, and catch rates in a stock whose current status is unknown but where the possibility of overfishing cannot be ruled out. For the swordfish, the most recent maximum sustainable yield (MSY)-based reference points are uncertain for the Indian Ocean population as a whole, whereas the resource in the southwest Indian Ocean is overfished (IOTC[2]). Therefore an increase in effort or catch rates (or both) on swordfish target fisheries may exacerbate the problem because local depletion has been observed in the past decade and biomass still remains below the level that would produce MSY. Additionally, the human dimension (i.e., socioeconomics) should also be considered, because both species (i.e., swordfish and blue shark) are important to fishermen and represent over 90% of the overall retained catch. A combination of management measures (e.g., spatial or seasonal protection of critical habitats and good practices in handling specimens to be released) may represent a more appropriate solution to efficiently mitigate the incidental bycatch and mortality of species (namely sharks) captured in pelagic longline fisheries.

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Patterns of movement, growth, and survival of adult sablefish (*Anoplopoma fimbria*) at contrasting depths in slope waters off Oregon

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Abstract—Demersal fish inhabiting continental slopes experience colder temperatures, increasing hydrostatic pressure, decreasing oxygen saturation, and decreasing productivity with increased depth. We examined depth-related patterns in small- and large-scale movement, growth, and relative survival of sablefish (*Anoplopoma fimbria*) tagged during 1996–2004 in Oregon waters at depths of 141–1225 m; 2614 of 17,400 fish were recaptured as of December 2016. Recapture rates indicated significant size-dependent mortality. Discard mortality was affected by surface temperature for small fish (<55 cm in fork length [FL]) from upper slope depths (<400 m). Depth effects on recapture rates reflected differences in fishing effort. Most recaptures were near the initial capture depth. Although 91% of the recaptures were within 200 km of the tagging location, some individuals migrated thousands of kilometers, reaching the western Aleutian Islands. Growth rates were faster for females than for males and decreased with depth. Sablefish in the deepest depths sampled had extremely slow growth rates (<2 cm FL/year), low dispersal (2.4%), and were largely female (81%). Prior studies of age distribution indicate that deep slope habitats also support greater longevity, potentially providing a refuge for older fish and a buffering effect to longevity overfishing, depending on spatial differences in exploitation rates.

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Sablefish occupy a remarkably broad geographic range in outer shelf and slope waters of the northern Pacific Ocean, from southern Baja California around the Pacific Rim to the coast of Japan (Hart, 1973). Mature adults typically occur at depths >100 m, and some occur at depths >2700 m (Beamish et al.[1]). Sablefish are broadcast spawners, releasing eggs at slope depths from January through March in waters of British Columbia, Canada (Mason et al., 1983), and from November through March in Oregon waters (Macewicz and Hunter, 1994). Larval and early juvenile stages occur in the neuston (upper few meters) layer (Shenker, 1988). In southeast Alaska and British Columbia waters, juveniles often migrate inshore and occupy shallow bays and sounds (Rutecki and Varosi, 1997). From Washington through California, juveniles settle to demersal habitats but typically remain offshore (Heyamoto and Alton, 1965). Adults have slow growth, low mortality, and life spans up to 114 years (Beamish and McFarlane, 2000). Much of the adult habitat occurs along a depth gradient of decreasing oxygen saturation, decreasing temperatures, and decreasing productivity.

The sablefish population is thought to comprise 2 stocks: a northern or Alaska stock, ranging from northwest Vancouver Island through the Aleutian Islands and Bering Sea to Japan, and a southern or west coast stock, ranging from southwest Vancouver Island to Baja California (Kimura et al., 1998). The 2 stocks differ in growth rates and life history parameters, including size and age at maturity. Northern fish attain larger asymptotic sizes, estimated as 67.7 cm in fork length (FL) for males and 80.1 cm FL for females (Echave et al., 2012), whereas estimates for southern fish are 56.3 cm FL for males and 64.2 cm FL for females (Johnson et al.[2]); however, there is considerable

[1] Beamish, R. J., C. Houle, C. Wood, and R. Scarsbrook. 1979. A summary of sablefish tagging and exploratory trapping studies conducted during 1978 by the Pacific Biological Station. Can. Data Rep. Fish. Aquat. Sci. 162, 113 p. [Available from website.]

[2] Johnson, K. F., M. B. Rudd, M. Pons, C. A. Akselrud, Q. Lee, F. Hurtado-Ferro, M. A. Haltuch, and O. S. Hamel. 2016. Status of the U.S. sablefish resource in 2015, 176 p. Pacific Fishery Management Council, Portland, OR. [Available from website.]

variability within regions and by depth (Echave et al., 2012; Head et al., 2014). Size and age at maturity have also been found to differ with latitude and depth; for females in the southern stock, Head et al. (2014) estimated 50% maturity at ages of 4.9–11 years and lengths of 48.5–58.5 cm FL.

The separation between sablefish stocks along the coast of Vancouver Island occurs at the boundary between the California Current upwelling ecosystem to the south and the Gulf of Alaska downwelling ecosystem to the north. The associated differences in a broad suite of oceanographic factors are likely to affect sablefish biology. Genotypic differentiation, however, is weak (Tripp-Valdez et al., 2012), indicating significant exchange between the 2 stocks of fish. Prior tagging studies have reported small but persistent migrations from Alaska to west coast waters and vice versa (Fujioka et al., 1988; Kimura et al., 1998; Echave et al., 2013).

Patterns in depth distribution

The broad bathymetric distribution of sablefish is thought to arise from an ontogenetic migration to progressively deeper depths with age, on the basis of increasing proportions of mature fish at greater depths (Fujiwara and Hankin, 1988), increasing mean length with depth (Hunter et al., 1989), and increasing abundances of older or larger fish with depth (Saunders et al., 1997; Sigler et al., 1997; Jacobson et al., 2001; Head et al., 2014; Johnson et al.[2]). Maloney and Sigler (2008) examined depth changes of tagged juveniles and found a clear pattern of movement to deeper waters by age 3 and a decline in occurrence at depths <500 m as fish aged. However, at ages from 3 to 20 years the largest concentration of each age class was at depths of 500–700 m. Kimura et al. (1998) compared depth at initial capture with depth at recapture and found that northern fish congregated at depths of 400–800 m, whereas southern fish were more likely to be recaptured in the same depth zone as that of tagging.

An alternative to the hypothesis of ontogenetic migration to deeper habitats was proposed by Norris (1997), who suggested that different depth distributions are a consequence of adaptive radiation of enzyme systems and differing physiological efficiency at different depths depending on genotype. Under this scenario, upon reaching sexual maturity, adults of different ecotypes migrate to depth ranges appropriate to their physiology and then remain at those depths. Fujiwara and Hankin (1988) likewise suggested the possibility of depth-related population structure for sablefish in California on the basis of contrasting maturity schedules.

The depth range of adult sablefish includes the persistent oxygen minimum zone (OMZ) present along the eastern Pacific slope. Gilly et al. (2013) defined the OMZ as waters with dissolved oxygen levels <20 µmol/kg, or approximately 10% of the saturation of oxygen in surface waters. The position of the OMZ varies latitudinally, but along the Oregon coast it spans depths of about 500–1500 m and is enveloped by an oxygen limited zone of slightly higher dissolved oxygen concentrations (Pierce et al., 2012; Gilly et al., 2013). Sablefish residing within the OMZ appear to be well adapted to the harsh physical conditions and potentially limited food availability of deep slope habitats (Sullivan and Smith, 1982; Drazen, 2007).

Spatial movement patterns

Spatial movements of sablefish have been extensively documented in tag–recapture studies. Within the northern stock, multiple studies spanning several decades have found widespread movement away from the location of tagging and that the likelihood of movement increases from southeast Alaska waters through the central Gulf of Alaska and into the Aleutian Islands and Bering Sea (reviews in Echave et al., 2013; Hanselman et al., 2015). In contrast, southern sablefish exhibit more limited movement away from the general tagging location (Fujioka et al., 1988; Kimura et al., 1998). Movement patterns of fish tagged in British Columbia waters suggest a more limited dispersal from southern tagging locations than from northern tagging locations (Beamish and McFarlane, 1988; McFarlane and Saunders, 1997).

Growth

Age-0 sablefish exhibit extremely rapid growth rates (Boehlert and Yoklavich, 1985; Sigler et al., 2001; Sogard and Olla, 2001; Sogard, 2011), but growth slows markedly in mature adults, and fish reach asymptotic size within their first decade (Johnson et al.[2]). Males grow more slowly than females (McFarlane and Beamish, 1983; Sasaki, 1985; Kimura et al., 1993; Saunders et al., 1997; Echave et al., 2012; Morita et al., 2012), and northern fish appear to have faster growth rates and attain larger sizes than southern fish (Kimura et al., 1993; Kimura, 2008). Depth-related differences in growth rates are suggested by the pattern of smaller size-at-age with depth (Saunders et al., 1997; Head et al., 2014).

Management impacts

The southern stock has been heavily exploited since the 1970s, although regulations have reduced annual landings to <10,000 metric tons (t) in recent years (Johnson et al.[2]). In conjunction with a size-related price structure, discarding of smaller fish was common practice. Although sablefish lack swimbladders and do not suffer barotrauma, they are susceptible to the rapid temperature increases associated with capture in cold, deep water and retrieval to warm surface waters. Mortality rates in experiments simulating capture at 4–6°C and discarding at surface temperatures

Table 1

Releases of tagged sablefish (*Anoplopoma fimbria*) off Newport, Oregon, from February 1996 to May 1998 (tagging set 1), with gear used, depth of sampling (in meters), surface temperature, fish sizes (measured in fork length [FL]), number of fish tagged, and number of fish recaptured for each sampling trip.

	Trip (month/year)						
	2/96	3/96	5/96	6/96	10/96	9/97	5/98
Gear	Trawl	Trawl	Trawl	Trawl and pot	Pot	Trawl	Trawl
Depth range (and mean)	371–644 (460)	431–565 (506)	221–293 (240)	141–631 (214)	421–581 (503)	227–649 (347)	221–406 (265)
Mean surface temperature (°C)	12.2	11.4	12.9	14.4	14.3	18.3	12.7
Number of fish tagged	42	139	2221	3002 (2913 trawl, 89 pot)	1977	48	80
Size range (cm FL)	40.8–77.9	46.8–75.9	34.8–83.5	30.7–81.5	44.5–83.5	41.4–80.3	41.9–81.0
Mean size (cm FL)	56.2	54.3	48.1	49.7	57.8	54.3	53.6
Number of recaptured fish and percentage of total fish tagged	5 (11.9%)	24 (17.3%)	322 (14.5%)	393 (13.1%)	489 (24.7%)	8 (16.7%)	13 (16.2%)

of 12–20°C indicate that discarded fish may fare poorly during periods of elevated surface temperatures (Olla et al., 1998; Davis et al., 2001). The additional stress imposed on fish caught in deeper waters may also increase discard mortality rates. Current management objectives have resulted in a greater spread of fishing effort throughout the year, but survival of discarded fish remains a concern in stock assessments. For example, total discards in the southern stock in 2013 were approximately 755 t, and applied mortality rates were 20% for fixed-gear fisheries and 50% for trawl fisheries (Somers et al., 2014).

Objectives

Our objectives were to examine patterns of movement, growth, and survival for sablefish residing in slope waters off central Oregon. We examined small-scale movements among depths and large-scale movements associated with long distance migrations, comparing the latter to prior studies of the 2 sablefish stocks. Tagging of fish captured at discrete depths and contrasting surface temperatures allowed us to examine the potential effects of temperature and depth on discard mortality. Growth rates were compared by depth and in relation to migration distances. All patterns were compared in relation to initial fish size, sex, and time at large, where possible.

Materials and methods

Fish capture and tagging

All tagging was conducted off Newport, Oregon. For the first tagging event (tagging set 1), fish were captured primarily in trawls from 4 chartered fishing vessels during 8 trips from February 1996 to May 1998 (Table 1). Fish were measured, tagged with a uniquely numbered Floy FD-94[3] nylon spaghetti tag (Floy Tag Inc., Seattle, WA) inserted on the left side just beneath the anterior end of the first dorsal fin, and immediately released. The goal of this tagging effort was to provide data for a preliminary evaluation of growth, as well as small- and large-scale movements. Boat captains selected fishing locations to maximize the number of fish available for tagging. A range of depths along the outer shelf and upper slope was sampled, with depths clustered within 2 groups, designated as depth zone 1, which represented fish captured at depths of 141–302 m, and depth zone 2, which represented fish captured at depths of 335–649 m.

For tagging set 2, fish were captured with pots deployed from 1 vessel at 2 depth ranges (327–366 m and 1112–1225 m) during 2 trips with expected warm (September 2003) and cool (May 2004) surface temperatures (Table 2). Depths were designated as depth zone 2 (to match tagging set 1) and depth zone 3. One objective of the sampling design was to test for effects of depth and surface temperature on discard mortality. The numbers of fish tagged were evenly distributed among the 4 depth and surface temperature combinations to provide a balanced design. Surface temperatures were measured during tagging, and bottom temperatures were estimated with the Simple Ocean Data Assimilation data set (Carton et al., 2005) and obtained from the Environmental Research Division Data Access Program server of the NOAA Southwest Fisheries Science Center (website).

Recaptured fish were reported by commercial fishermen, observers, and processors, with varying levels of information. For each analysis described below, re-

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2

Releases of tagged sablefish (*Anoplopoma fimbria*) off Newport, Oregon, in September 2003 and May 2004 (tagging set 2), with mean depth of sampling, surface temperature, fish sizes (measured in fork length [FL]), number of fish tagged, and number of fish recaptured for each sampling trip. All fish were captured with pots from the same vessel.

	Trip (month/year and depth zone)			
	9/03 zone 2	9/03 zone 3	5/04 zone 2	5/04 zone 3
Mean depth (m)	355	1145	353	1163
Surface temperature category and mean	Warm, 15.9°C	Warm, 16.9°C	Cool, 14.6°C	Cool, 14.5°C
Number of fish tagged	2460	2486	2463	2482
Size range (cm FL)	42.5–85.5	44.0–90.0	44.5–78.0	46.5–87.5
Mean size (cm FL)	54.3	57.7	57.4	60.1
Number of recaptured fish and percentage of total tagged	435 (17.7%)	140 (5.6%)	594 (24.1%)	191 (7.7%)

capture data were used depending on the availability and precision of information reported. Sample sizes are noted for each analysis in the results section. Where practical, recaptures from both tagging sets were combined for analysis.

Data analysis

The potential roles of fish size and initial capture depth on the probability of recapture were tested with logistic regressions conducted separately for each tagging set and by using the following equation:

$$\text{Logit}\,(P(x)) = \alpha + \beta_1 X_1 + \beta_2 X_2, \quad (1)$$

where $P(x)$ = probability of recapture;
X_1 = initial fish length (continuous variable);
X_2 = depth zone of initial capture (categorical variable);
α = a constant; and
β = a coefficient.

For tagging set 2, additional logistic regressions tested recapture rates between warm and cool surface temperatures (categorical variable) at the time of tagging. Initial inspection of these data suggested that surface temperature effects were more evident in smaller fish; therefore, logistic regressions were conducted separately for small (<55 cm FL), medium (55–65 cm FL) and large (>65 cm FL) size classes within each depth zone. These categories correspond with the size groups tested by Davis et al. (2001) for the rate of body core temperature increase after transfer to warmer water. Regressions for comparisons of recapture probability by surface temperature were calculated with this equation:

$$\text{Logit}\,(P(x)) = \alpha + \beta_1 X_1, \quad (2)$$

where X_1 = a temperature category.

For all logistic regressions, the Wald statistic was used to determine significance of each coefficient.

Analysis of small-scale movement among depths was possible for 1762 fish. We used analyses of covariance (ANCOVAs) calculated separately by initial depth zone to test for effects of recapture season (spawning: from November through April and nonspawning: from May through October) on recapture depth, with fish size and time at large included as covariates.

For recaptured fish with location coordinates, great circle distances from tagging to recapture location were calculated. We divided recaptured fish into residents, defined as fish recaptured within 200 km of their tagging locations, and "dispersers," fish recaptured >200 km from their tagging locations, according to Beamish and McFarlane (1988). Fish without precise location coordinates could be categorized as dispersers or residents on the basis of the general area of recapture; for example, fish caught in Alaska waters were dispersers regardless of their exact capture location. Using chi-square association tests and analysis of variance (ANOVA), we examined characteristics of these fish to determine whether the tendency to make long migrations from the tagging location was influenced by fish size, sex, or the depth of initial capture. We used linear regression to determine whether the proportion of fish dispersing was affected by the time at large.

We compared the growth of individuals whose recapture length and sex had been recorded, as well as recapture depth and gear used. Growth was expected to be influenced by fish size, with smaller fish growing at a faster rate than larger fish, and by time at large, with growth rate decreasing as the time at large increased. To select an appropriate growth model we first considered several age-based models that have been reparameterized for size-based application to tag-recapture data, including von Bertalanffy, Gompertz, and Schnute growth models, as described by Francis (1995), and a nonlinear regression model described for sable-

fish by Kimura et al. (1998). All produced comparable results that defined the roles of initial size and time at large on growth. Because our objective was to assess potential effects of different environmental factors, we elected to use the nonlinear regression approach, which provided a simple means of incorporating additional parameters into the model and evaluating their influence. We anticipated that depth would influence growth rates, with reduced growth at the deepest depths sampled due to low temperatures, low oxygen levels, and low food availability. We also anticipated that recapture gear could affect growth because Kimura et al. (1993) had observed higher growth for sablefish caught in pots than in trawls. Preliminary analyses indicated that growth of fish recaptured by longline was similar to that of fish recaptured in pots; therefore, the groups of fish captured by the 2 fixed gears were combined for comparison with fish recaptured in trawls.

We used a "best subsets" approach to evaluate the potential role of independent variables in growth, first including all factors in the nonlinear regression, then estimating subset models with individual factors removed. Because the growth model was not based on an explicit likelihood calculation, it was not readily adaptable to the commonly used Akaike information criterion approach for model comparison. Therefore, Mallows's C_p (Mallows, 1973), an appropriate metric of model fit for least squares regression, was calculated to compare among different formulations of the model in order to evaluate support for the different potential explanatory variables. The full model, with 6 parameters, was based on the following equation:

$$FL2 = FL1 + days * exp\,(\beta_1 * FL1 + \beta_2 * days + \beta_3 * sex + \beta_4 * depth1 + \beta_5 * depth2 + \beta_6 * gear), \quad (3)$$

where $FL1$ = initial fork length;
$FL2$ = recapture fork length;
$days$ = days at large;
sex = a dummy variable for sex (0=female, 1=male);
$depth1$ = depth at initial capture;
$depth2$ = depth at recapture;
$gear$ = a dummy variable for recapture gear (0= fixed, 1=trawl); and all β are coefficients.

We then evaluated all possible subset models with 1–5 parameters and calculated Mallows's C_p for each to evaluate how well each model balanced parsimony and fit to the data. The full model has C_p equal to the number of parameters by definition, whereas subset models that adequately account for variance in the data set but with fewer parameters will have a C_p that closely matches their reduced number of parameters. We examined the C_p values to determine if a simpler model (i.e., one with fewer parameters) was appropriate for describing growth differences.

We also examined growth of dispersing individuals to determine whether their growth rates differed from those of fish categorized as residents and whether growth varied with the distance moved. We used residuals from the full growth model in ANOVAs, conducted separately by sex, to first compare growth of dispersing fish with growth of resident fish. For the dispersers only, linear regressions were then used to compare growth with the distance moved.

All statistical analyses were performed with SYSTAT, vers. 13, software (Systat Software Inc., San Jose, CA).

Results

Initial size distributions

Size distributions at tagging differed by depth zone (Figs. 1 and 2). For the first set (1996–1998), 5291 fish were tagged from depth zone 1 and 2218 fish from depth zone 2. For the second set (2003–2004), 4923 fish were tagged from zone 2 and 4968 from zone 3. In zone 1 there were 2 clear size modes at 34 cm and 44 cm FL (tagging set 1, Fig. 1) that were not present in the deeper zones. In zones 2 and 3, fish sizes followed a continuum, likely representing a broad range of fish ages. Modal size was larger (57 cm FL) in zone 3 than in zone 2 (54 cm FL). Very large fish (≥70 cm FL) occurred at all depths but were relatively rare overall, with n=56 in zone 1 (1.1% of total), n=130 in zone 2 (1.8%) and n=47 in zone 3 (0.9%).

For both tagging sets combined, sex was determined for 690 recaptured fish. The sex ratio varied with initial capture depth, ranging from 58% females in depth zone 1 to 62% in depth zone 2 and 81% in depth zone 3, indicating an increasing bias toward females at increasing depths.

Probability of recapture

In total, 2614 tagged fish were recaptured up to December 2016, with 1254 (16.7%) from tagging set 1 and 1360 (13.7%) from tagging set 2. The potential roles of fish size and initial capture depth on the probability of recapture were tested with logistic regressions, conducted separately for each tagging set. For tagging set 1, recapture rates increased with fish size (Wald statistic: 10.4, P<0.001) and were greater in depth zone 2, with 23.6% fish recaptured, than in zone 1, with 13.8% fish recaptured (Wald statistic: 4.4, P<0.001). For tagging set 2, recaptures again increased with fish size (Wald statistic: 13.7, P<0.001), but were greater in zone 2 (20.9%) than in zone 3 (6.7%, Wald statistic: 22.1, P<0.001).

One of the objectives with tagging set 2 was to determine whether discard mortality is influenced by depth of capture or by the temperature gradient experienced by fish captured in cold deep waters and released in warm surface waters. Tagging set 1 was not included in this comparison because of limited sampling at warm surface temperatures and deeper depths. For tagging set 2, recapture rates differed markedly between depth

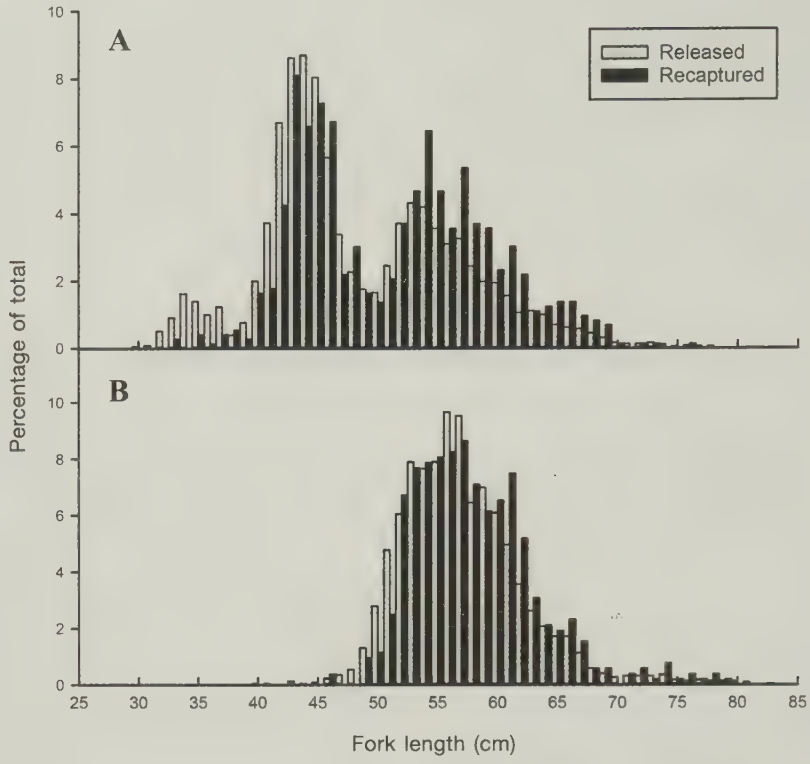

Figure 1

Initial size distributions as a percentage of the total number of fish for tagged (released) and recaptured sablefish (*Anoplopoma fimbria*) captured in shelf and slope waters off Newport, Oregon, from February 1996 to May 1998 (tagging set 1). Fish were divided into 2 groups on the basis of initial depth of capture: (**A**) depth zone 1 (141–302 m) and (**B**) depth zone 2 (335–649 m).

zones; therefore, the effects of surface temperature were evaluated separately for each depth category. Using logistic regressions, we compared recapture rates, by warm and cool surface temperature categories, for each size group of small, medium, and large fish within each depth zone. A significant difference for zone 2 fish was found only for small fish, with the probability of recapture increasing when surface temperatures at tagging were cooler (Table 3; Wald statistic: 4.4, $P<0.001$). For fish initially captured in zone 3, there were no significant differences between recapture rates of small, medium, or large fish for the tagging temperature categories. However, the sample size for small fish was only a total of 25 recaptured fish and therefore limits our confidence in this result.

Small-scale movements among depths

Fish initially captured in depth zone 1 tended to be recaptured at deeper depths, with recaptures at depths from 124 to 1207 m (Figs. 3 and 4). However, 55% of the recaptures were at depths within 200 m of the initial capture depth. Fish were recaptured at greater depths during the spawning season (from November through April) than during the nonspawning season (ANCOVA: $F_{1,438}=26.6$, $P<0.001$). Recapture depths increased with time at large ($F_{1,438}=29.4$, $P<0.001$) but did not differ with fish size ($F_{1,438}=1.8$, $P=0.184$). Fish initially captured in depth zone 2 were recaptured at depths from 73 to 1220 m; however, 86% of the recaptures were within 200 m of the initial depth. As observed for fish from depth zone 1, depth of recapture was greater during the spawning vs. nonspawning season (ANOVA: $F_{1,1054}=68.1$, $P<0.001$), recapture depth increased with time at large ($F_{1,1054}=64.4$, $P<0.001$), and there was no effect of initial fish size ($F_{1,1054}=3.0$, $P=0.081$). Fish initially captured in zone 3 tended to be recaptured near their original depth or shallower, at depths from 238 to 1280 m; 56% were recaptured within 200 m of their initial depth. In contrast to the result for fish from the shallower depth zones, recapture depth of zone 3 fish did not differ by season (ANOVA: $F_{1,253}=0.2$, $P=0.698$). Recaptures tended to be deeper with both increasing time at large ($F_{1,253}=83.6$, $P<0.001$), and with larger initial fish size ($F_{1,253}=27.6$, $P<0.001$).

Table 3

Results of logistic regressions for comparing recapture rates of small (<55 cm in fork length [FL]), medium (55–65 cm FL), and large (>65 cm FL) sablefish (*Anoplopoma fimbria*) initially captured off Newport, Oregon, in depth zones 2 (mean depth: 354 m) and 3 (mean depth: 1154 m) at warm (mean 16.4°C) and cool (mean 14.5°C) surface temperatures for tagging set 2 (September 2003 and May 2004).

Size class	Depth zone	Number tagged at warm temp.	Number (%) recaptured at warm temp.	Number tagged at cool temp.	Number (%) recaptured at cool temp.	Wald statistic	*P*
Small	2	1608	183 (11.4%)	726	131 (18.0%)	4.3	<0.001
Small	3	674	17 (2.5%)	208	8 (3.8%)	1.0	0.314
Medium	2	693	207 (29.9%)	1571	417 (26.5%)	1.6	0.111
Medium	3	1635	105 (6.4%)	1886	132 (7.0%)	0.7	0.496
Large	2	156	45 (28.8%)	165	46 (27.9%)	0.2	0.847
Large	3	172	18 (10.5%)	370	50 (13.5%)	1.0	0.320

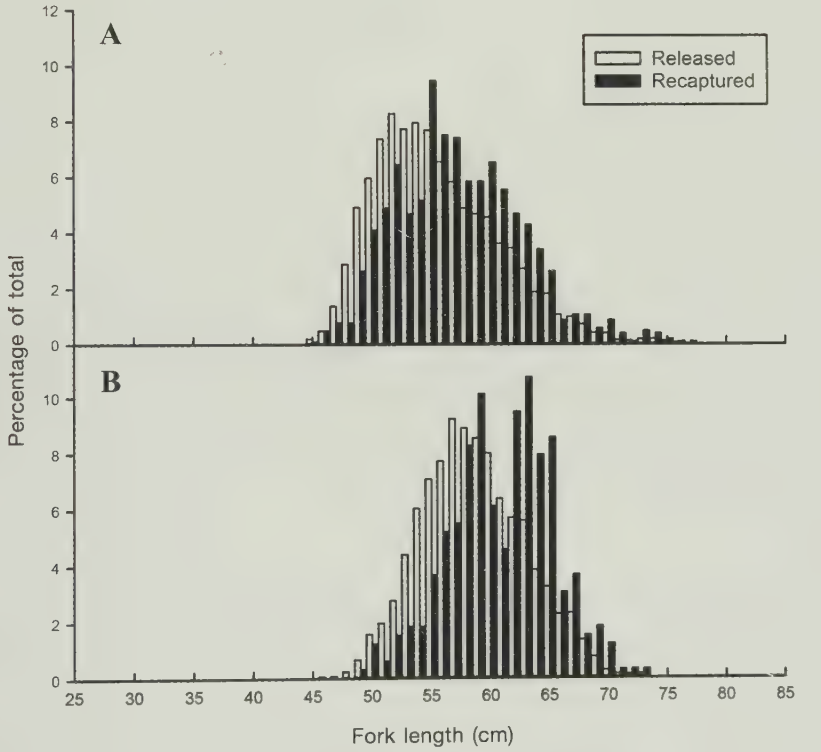

Figure 2

Initial size distributions as a percentage of the total number of fish for tagged and recaptured sablefish (*Anoplopoma fimbria*) captured in slope waters off Newport, Oregon, in September 2003 and May 2004 (tagging set 2). For this tagging set, 2 discrete depth zones were targeted for initial captures: (**A**) depth zone 2 (327–366 m) and (**B**) depth zone 3 (1112–1225 m).

Large-scale movements

For both sets of tagging combined, 2566 recaptured fish had sufficient location information to categorize them as dispersers or resident fish (recaptured >200 km or <200 km from the tagging location, respectively). Dispersers composed only 9% of these fish. Of the fish whose sex was reported, there was a marginal but

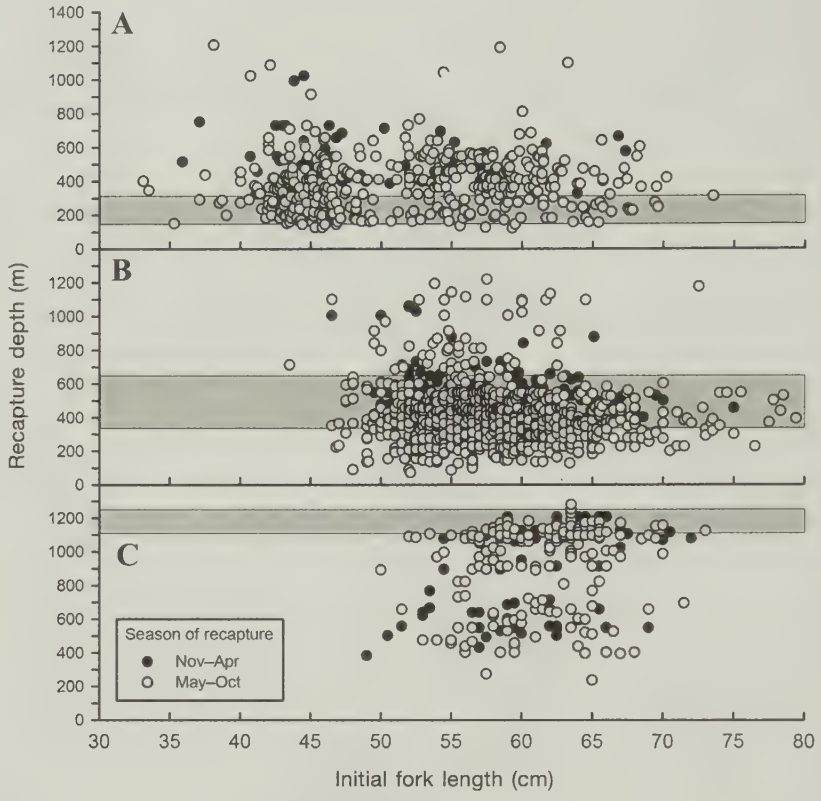

Figure 3

Recapture depth for sablefish (*Anoplopoma fimbria*) initially tagged in (**A**) depth zone 1 (141–302 m), (**B**) depth zone 2 (327–649 m), and (**C**) depth zone 3 (1112–1225 m) off Newport, Oregon, during 1996–1998 (tagging set 1) or 2003–2004 (tagging set 2) by initial fork length (in centimeters). Gray boxes indicate the range of depths at tagging. Fish from both tagging sets are combined. Solid symbols denote fish recaptured during the spawning season (November–April) and open symbols denote fish recaptured in the nonspawning season (May–October).

nonsignificant trend for females to be more likely to disperse than males (χ^2=3.47, P=0.062). In contrast, depth of initial capture had a highly significant effect, with fish from depth zone 3 rarely recaptured far from their tagging location (Fig. 5A; χ^2=20.7, P<0.001). The proportion of recaptured fish that had dispersed from the tagging location increased with increased time at large (regression of proportion dispersers vs. years at large with years 14–19 combined: $F_{1,13}$=30.2, P<0.001). For all recaptured fish at large at least 10 years (n=98), 15% were categorized as dispersers.

Dispersers tended to be smaller at initial capture than resident fish. This trend was significant for all fish combined (ANOVA: $F_{1,2559}$=26.1, P<0.001). For the smaller set of fish with known sex, the trend was significant for females ($F_{1,437}$=21.4, P<0.001) but not for males ($F_{1,238}$=0.6, P=0.453). In addition, within dispersers, smaller fish tended to migrate to greater distances than larger fish for all fish combined (Fig. 6; regression: $F_{1,218}$=15.6, P<0.001, coefficient of determination [r^2]=0.07) as well as for females only ($F_{1,87}$=11.6, P=0.001, r^2=0.11) and for males only ($F_{1,33}$=7.2, P=0.011, r^2=0.16).

Fish that migrated away from the tagging area tended to move north and around the Pacific Rim (Fig. 7). Only 15% of the dispersers traveled south, and few of these moved more than 400 km; the most southern recapture location was Bodega Canyon, California, a straight line distance of about 800 km. Fish that traveled north and northwest were recaptured throughout the available geographic range of slope waters up to the western Aleutian Islands, and the most distant recaptures occurred near Tanaga Island, approximately 4000 km as straight line travel, but presumably far greater if fish travel along depth contours. Eight fish were recaptured on seamounts off the west coast of the United States and Canada (7 fish in the vicinity of Brown Bear and Cobb and 1 on Bowie). An effect of

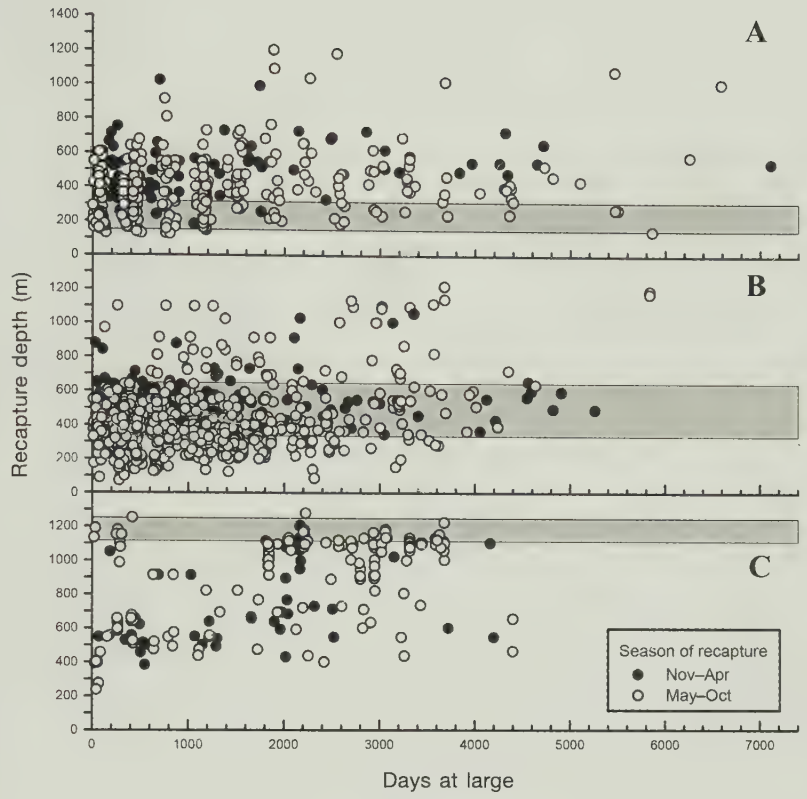

Figure 4

Recapture depth for sablefish (*Anoplopoma fimbria*) initially tagged in (**A**) depth zone 1 (141–302 m), (**B**) depth zone 2 (327–649 m), and (**C**) depth zone 3 (1112–1225 m) off Newport, Oregon, during 1996–1998 (tagging set 1) or 2003–2004 (tagging set 2) by time at large in days. Gray boxes indicate the range of depths at tagging. Fish from both tagging sets are combined. Solid symbols denote fish recaptured during the spawning season (November–April) and open symbols denote fish recaptured in the nonspawning season (May–October).

initial capture depth was also evident in the distance moved; no fish from depth zone 3 traveled farther than 700 km (Fig. 5B).

Growth

Recapture reports with information on sex, size, depth, and gear were available for 357 females and 181 males. Sample sizes by depth zone were 68, 188, and 101 females and 51, 108, and 22 males for depth zones 1, 2, and 3, respectively. Application of the full nonlinear regression model incorporating initial fish size, days at large, sex, initial capture depth, recapture depth, and recapture gear accounted for a substantial level of variation in growth (r^2=0.79; Table 4). All subset models excluding 1 or more parameters provided inferior explanatory power, with values of Mallows's C_p far exceeding the number of parameters (all C_p estimates >30), indicating that the full model was the best supported descriptor of the data (Table 5). To illustrate these effects we plotted growth estimates from the full model while setting the time at large to 1 year, recapture gear as fixed gear, and tagging and recapture depths as the midpoint of each depth zone. Growth increments were calculated separately by sex for the range of initial fish sizes observed for recaptured fish from each depth zone (Fig. 8). As expected, small fish grew faster than large fish, and females grew faster than males. Based on model estimates, growth rates were lower by 42% for males than for females. Growth also was substantially lower with increasing depth. Holding fish size constant and using the midpoint of each depth zone, we found that fish in zone 2 grew about 36% more slowly than fish in zone 1. Growth rates of fish in zone 3 were reduced by 68% compared with growth rates of fish in zone 2, and by 79% compared with growth rates of fish in zone 1. Fish recaptured in trawls had growth rates about 22% lower than those of fish recaptured by fixed

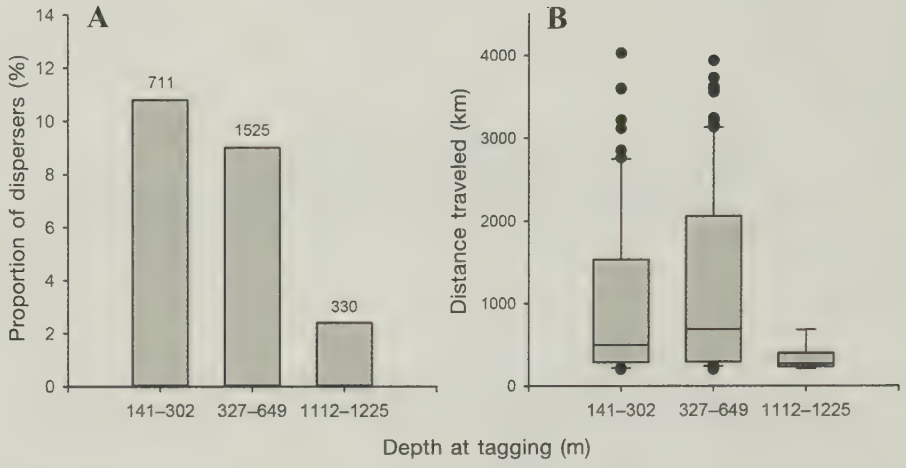

Figure 5

(**A**) Proportion of sablefish (*Anoplopoma fimbria*) that moved >200 km from their tagging location (dispersers) for each of 3 depth zones at tagging off Newport, Oregon, during 1996–1998 (tagging set 1) or 2003–2004 (tagging set 2). Fish at large for <1 year were excluded. The number of recaptured fish with reliable location information is given above each bar. (**B**) Distance traveled (great circle distance between tagging and recapture location) by dispersing fish (exclusive of all residents, fish that moved <200 km from their tagging location) for each depth zone at tagging. Box plots show median, 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers), and outliers. Fish from both tagging sets are combined.

gear (data not shown). For fish of the sizes initially captured in this study, expected annual growth peaked at about 8–9 cm FL/year for small females and 4–5 cm FL/year for small males in zone 1, declining to <2 cm FL/year for all fish of both sexes in zone 3.

To determine whether fish that dispersed gained a growth advantage compared with fish that were residents, we applied ANOVAs to residuals from the nonlinear growth model, evaluating each sex separately. There was no difference in growth of female fish that dispersed and those that were residents (ANOVA: $F_{1,355}$=2.1, P=0.148). In contrast, males that dispersed had significantly faster growth rates than male residents ($F_{1,178}$=6.0, P=0.015). In addition, for dispersed males, growth was positively correlated with the distance moved from the tagging location (regression: $F_{1,26}$=6.7, P=0.015). No relationship of growth with distance traveled was observed for female dispersers ($F_{1,67}$=0.3, P=0.590).

Discussion

Probability of recapture

Recapture rates in this study were higher than those of prior studies of tagged sablefish, with 16.7% of fish in tagging set 1 and 13.7% of fish in tagging set 2 recaptured. High recapture rates reflect the extended recapture period (up to 20 years for tagging set 1 and 13 years for tagging set 2), and the low natural mortality rate for sablefish (Johnson et al.[2]). The probability of recapture increased with fish size, as observed in prior studies (McFarlane and Beamish, 1990; Saunders et al., 1990; McFarlane and Saunders, 1997). Stachura et al. (2012), in contrast, found no effect of fish size on likelihood of recapture in southeast Alaska, but 88% of their fish were >60 cm FL. These patterns potentially reflect a nonlinear decrease in natural mortality rates with increasing fish size (e.g., Lorenzen, 1996).

The marked contrast in recapture rates between depth zones 2 and 3 of tagging set 2 was suggestive of a depth effect on discard mortality. However, this result was likely to be in part due to different fishing effort between depths. On the basis of logbook data reported to the Oregon Department of Fish and Wildlife, limited fishing effort occurred at depths >900 m throughout the time period after tag deployment. Overall during the years 2004–2014, fish captured at depths >900 m accounted for 5.3% of the total catch reported by trawl fisheries logbooks and 15.8% of fixed-gear fisheries. Although logbook compliance is not 100%, these estimates clearly suggest fishing effort in deeper habitats was much lower than in shallower waters. Fish tagged in zone 3 tended to be recaptured later in the time series, in contrast with fish from zone 2, which were recaptured at a steadily decreasing rate over the 13 postcapture years (Fig. 9). This contrast likely reflects increasing effort in deeper waters after 2008, particularly for fixed-gear fisheries. Based on depths of cap-

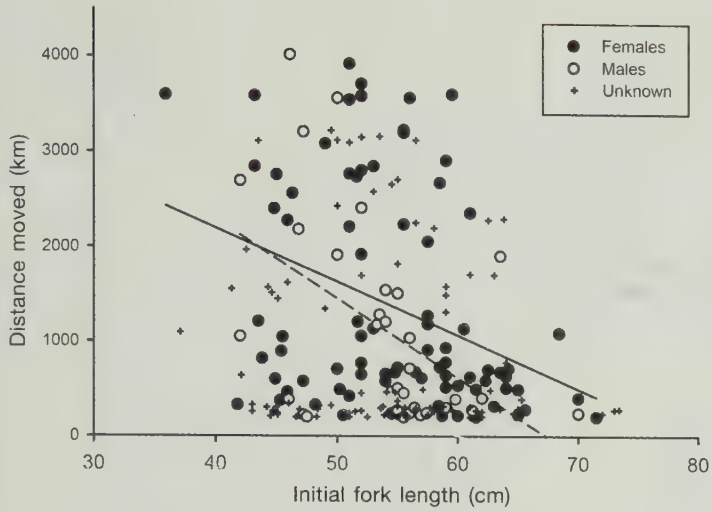

Figure 6

Relationship between initial size and distance moved (great circle distance between tagging and recapture location) for sablefish (*Anoplopoma fimbria*) initially captured off Newport, Oregon, during 1996–1998 (tagging set 1) or 2003–2004 (tagging set 2). Only fish that moved >200 km from their tagging location and had reliable recapture locations are included. Regression lines were calculated separately for females (solid) and males (dashed). Fish from both tagging sets are combined.

ture reported in logbooks and applied to total landings of sablefish in Oregon (all gears combined; Pacific Fisheries Information Network, website), annual landings in depths >900 m were <140 t before 2009, but >220 t during 2009–2013. Recapture rates after 2008 were 4.2% for fish tagged from zone 2 and 4.5% for fish tagged from zone 3 (after adjusting for removal of all previously recaptured fish). Thus, the low early recapture rates of fish tagged in zone 3 and the increasing recaptures after 2008 likely reflect patterns in overall fishing effort and therefore do not support a depth effect on discard mortality.

Recapture rates from the shallower end of the sablefish depth range may have been impacted by spatial closures. Offshore boundaries of the rockfish conservation areas varied spatially and temporally after their implementation in 2002 (Keller et al., 2014) and did not strictly match depth contours. In Oregon waters they were approximately 183 m (100 fm) for fixed gear and 274 to 457 m (150-250 fm) for bottom trawls from 2003 to present. Fish that were initially captured and remained after tagging in depth zones 1 and 2 would have continued to be vulnerable to fixed-gear fisheries but may have avoided trawl capture. The depth effect on probability of recapture for tagging set 1, with reduced recaptures in depth zone 1 compared with depth zone 2, may have been influenced, in part, by lower fishing pressure in the shallowest habitats.

Surface temperatures appeared to influence discard mortality only for small fish <55 cm FL, which were recaptured at significantly lower rates under warmer surface temperatures than under cooler surface temperatures in depth zone 2. Although the difference was not significant in zone 3, the overall recapture rate of small fish from zone 3 was very low (Table 3), limiting detectability of a temperature effect. No differences in recapture rates between surface temperatures were observed for medium or large fish at either depth. These size effects are consistent with prior laboratory studies. Observations of temperature-induced mortality were from experiments conducted primarily with fish <55 cm FL, for which body core temperatures increased at a faster rate than those of larger fish after transfer to warm water (Davis et al., 2001). Davis and Parker (2004) also observed size-dependent effects on susceptibility to postcapture stressors.

Implications of depth distribution

Our results corroborate those of other studies that indicate low abundance of immature fish in deeper slope habitats (Jacobson et al., 2001; Maloney and Sigler, 2008). Fish in the 2 small size modes captured during initial sampling in depth zone 1 did not occur in depth zones 2 or 3—a result consistent with a pattern of settlement in relatively shallow water (<300 m). Recaptures of these smaller fish occurred throughout the slope depth gradient, with 38% occurring >200 m deeper than the initial depth. Larger fish initially captured in zones 1 and 2 were likewise recaptured throughout the depth gradient, but only 17% were recaptured >200 m deeper than their initial depth. For fish initially captured in depth zone 3, 44% were recaptured at depths >200 m shallower than their initial depth. These results provide only a snapshot view of depth-related movements because there is no information on depth distributions between capture and recapture. However, if recapture depths reflect general depth preferences over time, they suggest that most fish remained relatively close to their initial depths within the time frame covered by this study. For fish initially captured in zones 1 and 2, there was no greater likelihood for smaller fish to be recaptured at deeper depths than larger fish, counter to our expectation of ontogenetic movement. The significant effect of initial size on recapture depths for fish from zone 3 was also counter to expectations, with smaller fish more likely than larger fish to be recaptured in shallower depths.

Some of these patterns were potentially biased by fishing effort; for example, low effort in deep slope waters would limit our detection of fish that moved to those depths. The marked increase in recaptures after 2008 of fish initially tagged in depth zone 3 (Fig. 9) presumably reflected increased fishing effort. Recap-

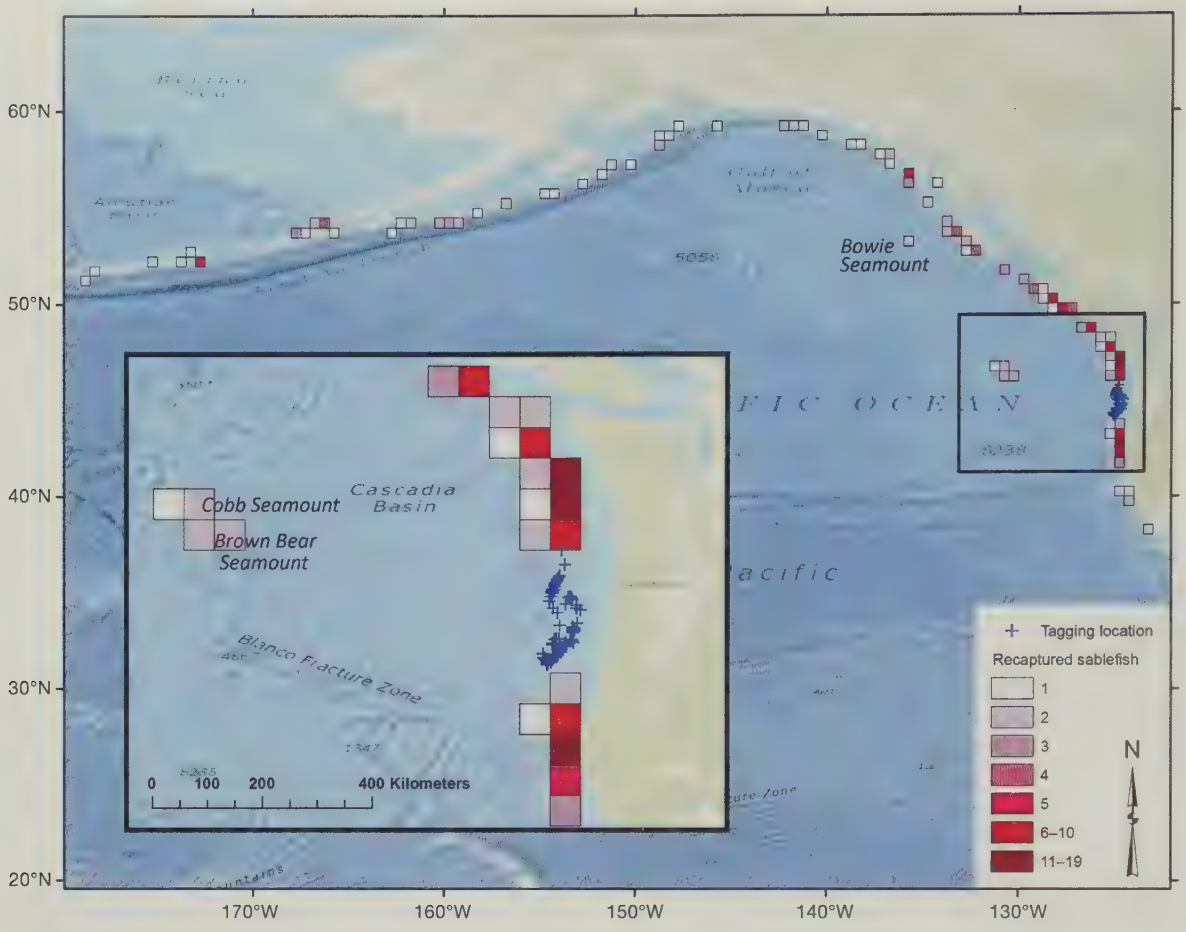

Figure 7

Location of all initial captures of sablefish (*Anoplopoma fimbria*) off Newport, Oregon, (blue crosses, inset map) and recapture locations of dispersers (fish that moved at least 200 km from their initial capture location) for the period 1996–2016. Recaptures are clustered into 0.5° grids to mask exact capture locations. Recapture locations of fish categorized as residents, fish that moved <200 km from their tagging location, are not shown. Fish from both tagging sets are combined.

ture rates in depths >900 m for fish initially captured in zones 1 and 2 also increased in conjunction with the increased fishing effort starting in 2009, providing evidence of some movement to deep slope habitats. Approximately 13% of all fish initially captured in depth zones 1 and 2 and recaptured after 2008 were caught at depths >900 m.

Over a time frame of 1–2 decades, our results suggest settlement of sablefish to shelf habitats, then subsequent movement to a broad range of different depths along the slope. For females caught in trawl surveys of the southern stock, mean age increased with depth, but the spread of ages also increased, with fish at the deepest depths sampled ranging from 6 to 59 years old (Head et al., 2014, fig. 2), suggesting a pattern of early movement to a broad range of depths. The absence of older females at shallower depths noted by Head et al. (2014) could arise from several processes. Fish could be moving progressively deeper with time but at very slow rates, as suggested for Dover sole (*Microstomus pacificus*) by Hunter et al. (1990). Fish could also be accelerating their depth-related movement as they age, resulting in an accumulation of older fish in deeper habitats. Alternatively, higher mortality rates in shallow than in deep habitats, either natural or fishing induced, could reduce the life span of fish residing in upper slope areas. A depth-related decline in natural mortality rates would be consistent with the hypothesized longevity benefits of residence in or near the OMZ, whereas a depth-related decline in fishing mortality would be consistent with observed differences in effort by depth, potentially resulting in fishing-induced age truncation in the more heavily exploited shallower habitats.

Seasonal differences in recapture depths for fish from zones 1 and 2 indicated occurrence of sablefish in deeper waters during the potential spawning season (November–April) than during the nonspawning months of May–October. These depth differences were relatively minor; for all recaptures from zones 1 and 2 combined, mean depths were 122 m deeper in spawning than in nonspawning months. However, they do suggest movement to deeper waters as spawning begins.

Table 4

Results of nonlinear regression for estimating recapture size of sablefish (*Anoplopoma fimbria*) as a function of initial size, time at large, sex, depth at initial capture, depth at recapture, and recapture gear. Growth data were available for 398 females and 203 males. Estimated parameter coefficients are listed along with their standard errors (SEs) and 95% confidence intervals (CIs).

Parameter	Estimated coefficient	SE	Lower 95% CI	Upper 95% CI
Initial size (fork length)	−0.002651	0.000098	−0.002843	−0.002459
Time at large (days)	−0.000223	0.000016	−0.000254	−0.000193
Sex (0=female, 1=male)	−0.539742	0.048204	−0.634437	−0.445048
Initial depth	−0.001105	0.000108	−0.001317	−0.000893
Recapture depth (m)	−0.000565	0.000090	−0.000741	−0.000389
Recapture gear (0=fixed, 1=trawl)	−0.251627	0.049858	−0.349570	−0.153684

Table 5

Coefficient of determination (r^2) and Mallows's C_p statistics for nonlinear regressions in estimating recapture size of sablefish (*Anoplopoma fimbria*) as a function of models including 1–6 independent variables. The model with the highest r^2 and lowest C_p values for each subset number of input variables is noted with an X, indicating variables included in the model.

	Number of input variables					
	6	5	4	3	2	1
C_p	6.0	33.9	81.3	332.5	687.4	900.5
r^2	0.789	0.776	0.756	0.693	0.577	0.503
Independent variable						
Initial size	X	X	X	X	X	X
Sex	X	X	X	X	X	
Initial depth	X	X	X	X		
Time at large	X	X	X			
Recapture depth	X	X				
Recapture gear	X					

For fish initially captured in depth zones 1 and 2, recapture depths indicated extensive movement within the upper slope region, but limited recaptures at depths within the OMZ. Only 10% of the total recaptures from zones 1 and 2 were at depths >600 m. Low oxygen environments may contribute to reduced growth rates but enhance longevity through reducing oxidation damage. Cailliet et al. (2001) found that within the speciose rockfishes (*Sebastes* spp.), deeper dwelling species had much longer life spans than shallower dwelling species. They suggested that the reduced metabolic rates of fish living in deep, low oxygen waters promote longevity by reducing exposure to oxidative stress. Thus, there may be a trade-off between growth and longevity for fish living above the OMZ in contrast with those fish living within it. This trade-off is suggested by the contrast between size and age distributions with depth observed for female sablefish by Head et al. (2014).

In our study, the sex ratio became increasingly biased toward females as depth increased, reaching 81% in depth zone 3 (1112–1225 m). Beamish et al.[1] observed a further skewed sex ratio in extremely deep waters off British Columbia, with 93% females in waters deeper than 1800 m. On the basis of our results and those of Beamish et al.[1] and Head et al. (2014), sablefish residing along the deep slope are primarily females with minimal growth, minimal propensity to disperse, and extended life spans. A disproportionate contribution of older or larger females to reproductive success has been documented for many long-lived species (Hixon et al., 2014). Rodgveller et al. (2016) found that older female sablefish in Alaska produced larger eggs and had an earlier start to the spawning season, although relative fecundity did not increase with age. In addition to these maternal effects on reproduction, there is clearly a potential for long life spans to buffer against longevity overfishing, or the removal of large numbers of older fish as described by Beamish et al. (2006). The relative inaccessibility and lower fishing effort in deep slope habitats suggests that they provide

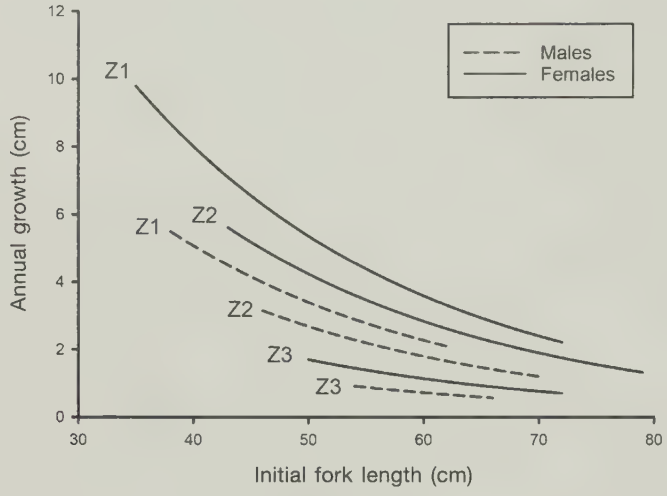

Figure 8

Estimated annual growth for male (dashed lines) and female (solid lines) sablefish (*Anoplopoma fimbria*) that resided in 3 depth zones (Z1=141–302 m, Z2=327–649 m, Z3=1112–1225 m) when they were initially captured off Newport, Oregon, during 1996–1998 (tagging set 1) or 2003–2004 (tagging set 2). Growth estimates were derived from the full nonlinear regression model (Table 4) with time at large set at 365 days, depth at both tagging and recapture set at the mid-depth within each zone, and recapture gear set at fixed gear. For each depth zone, the range of fish sizes was restricted to that observed for recaptured fish with known sex. Fish from both tagging sets are combined.

a refuge in which females can survive and reproduce over many years, capitalizing on periodic environmental regimes favorable to larval survival and production of strong year classes.

Implications of spatial movement patterns

In contrast with the northern stock of sablefish, long distance movements were much less evident in Oregon fish and consistent with prior studies of the southern stock (Dark, 1983; Wespestad et al., 1983; Fujioka et al., 1988; Kimura et al., 1998). After 13 (2003–2004 tagging) to 20 (1996–1998 tagging) possible years at large, only 9% of all recaptured fish were taken from locations >200 km from the tagging sites. Beamish and McFarlane (1988) found similar proportions of dispersers for fish tagged off Vancouver Island (fish that are likely to be part of the southern stock), but increasing dispersal for fish tagged off Haida Gwaii, Queen Charlotte Islands (fish that are likely to be part of the northern stock). The number of fish that dispersed from Oregon waters may have been underestimated if tag reporting differed by region. However, the nearly continuous geographic occurrence of recaptured dispersers across Alaska slope habitats (Fig. 7) and the high estimated levels of reporting, particularly in more recent years (Hanselman et al., 2015), suggest that Alaska fishermen are very cooperative in returning tags. Lower fishing effort and lower reporting rates in California waters may have resulted in reduced recovery of fish that moved south. For the years of possible recaptures in this study (1997–2016), sablefish landings in the California commercial fishery were on average 78% of the annual landings in Oregon (Pacific Fisheries Information Network, website). Because emigration rates appeared to increase over time and tag loss rates are cumulative, it is possible that some dispersers were not recognized because of tag loss. Overall, however, there was a clear tendency of Oregon fish to remain in Oregon waters, particularly for larger fish and fish residing in deeper habitats.

The fish that did disperse primarily traveled north and west, reaching almost to the farthest extent of U.S. waters in the western Aleutian Islands. Interestingly, dispersers from British Columbia waters also traveled primarily north into Alaska waters (Beamish and McFarlane, 1988). Although McFarlane and Saunders (1997) reported a number of recaptured fish in the Bering Sea for fish tagged in British Columbia waters, they did not report whether those fish were initially tagged off Haida Gwaii or Vancouver Island. Of the fish captured in Oregon waters in this study, none were recaptured in the Bering Sea.

There was an increased likelihood of migration with time at large, as with the results of Beamish and McFarlane (1988), but a few fish moved up to 2000 km within the first year after tagging, suggesting a high capacity and motivation for migration. The underlying reason for why some fish make extensive migrations, whereas others remain in the same general location for many years, is elusive. Morita et al. (2012) concluded that fish dispersing away from Bering Sea and Gulf of Alaska locations were mostly females that gained a growth advantage by migrating. We did not find a difference in growth between dispersing and resident females, but we did find a growth advantage for dispersing males. A propensity for dispersal may be related to individual differences in behavioral syndromes (Conrad et al., 2011). For example, intrapopulation differences in dispersal distances were found to be correlated with behavioral traits by Fraser et al. (2001) and Cote et al. (2010). Although dispersers are likely lost to their natal stocks, they maintain the metapopulation integrity of the species, and an extensive body of theory dating back to Hamilton and May (1977) argues for the fitness benefits of having some portion of a population disperse to different locations. This life history attribute of sablefish has clearly been successful considering their current geographic range.

Growth

Growth rates of recaptured fish generally matched previously observed patterns, with females growing faster than males, small fish growing faster than large fish,

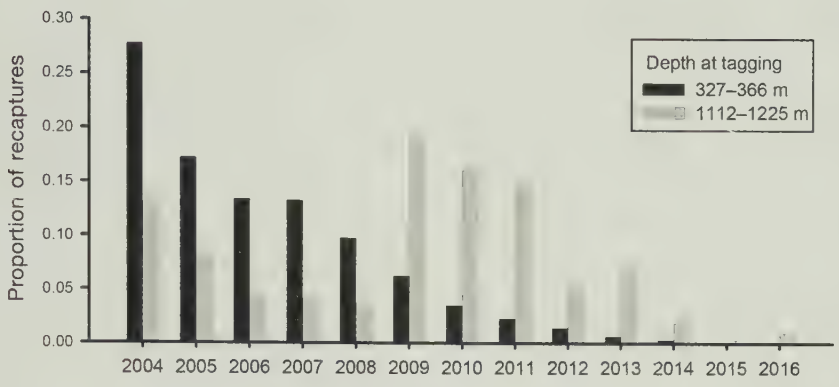

Figure 9

Proportion of all recaptured sablefish (*Anoplopoma fimbria*) initially captured in 2 depth zones during the second set of tagging (tagging set 2) for each year following release. Only resident fish that did not disperse more than 200 km from their tagging location are included.

and growth rates overall slowing with time at large. Estimated growth rates of males in the full model were 42% lower than those of females. We were also able to document greatly reduced growth for fish of all sizes residing at deeper depths (zone 3). The depth effect on growth has been suggested by decreasing size at age with depth for both males and females (Saunders et al., 1997; Head et al., 2014) and verified here by recaptures of fish that presumably spent the time between tagging and recapture primarily near the depth of initial capture. Initial fish sizes of recaptured fish available for growth estimation from depth zone 3 ranged from 50 to 70 cm FL for females and 54 to 66 cm FL for males—a size range that includes immature individuals and fish not expected to be close to their asymptotic size. Our results corroborate those of Head et al. (2014), who found a marked decrease in asymptotic size with increased capture depth for female sablefish residing in west coast slope habitats from Cape Mendocino, California, to the U.S.–Canada border. Reduced growth at deeper slope habitats could arise from 2 different mechanisms. First, individual differences in genetically determined intrinsic growth rates could be associated with depths selected by fish after settlement such that fish with inherently lower growth capacity migrate to deeper habitats than those of fish capable of faster growth rates. Under this scenario, these individuals would have lower asymptotic sizes regardless of their habitat. Alternatively, reduced growth rates in deep slope waters could reflect environmental conditions of low temperature, low dissolved oxygen levels, and low productivity. Under this scenario, fish have lower asymptotic sizes because of a limited opportunity for growth; they are unable to attain the asymptotic sizes of fish residing at shallower depths. Although the latter, environmentally based mechanism is perhaps more intuitively appealing, contrasting intrinsic growth capacity would be consistent with depth-dependent population structure as suggested by Fujiwara and Hankin (1988) and Norris (1997).

An additional factor influencing growth was the gear used at recapture; fish recaptured in fixed gear grew at faster rates than fish recaptured by trawls. Kimura et al. (1993) found a similar result and suggested a difference in selectivity between the 2 gear types. Sablefish actively entering baited traps or attacking bait on longlines may be more aggressive than fish captured passively by trawls. Individual differences in growth rates are often associated with behavioral differences in activity and boldness, potentially leading to differences in susceptibility to fishing gear (Biro and Post, 2008).

Caveats

As in any study of tag–recapture data that depend on tag returns primarily from commercial fishermen, there are several sources of potential error in interpretation of the resulting data. First, tag loss will result in recaptured fish not being identified. Prior studies of tag loss in sablefish with the use of double tag methods derived estimates of 0.02–0.03 for the instantaneous tag shedding rate per year (Beamish and McFarlane, 1988; Saunders et al., 1990; Lenarz and Shaw, 1997). Although these estimates are low compared with those reported for several other species (Lenarz and Shaw, 1997), over time the proportion of fish retaining their tag will decrease substantially. In our study, tag loss may have resulted in an underestimate of migration rates away from the tagging area over time, especially because the proportion of recaptured fish that were classified as dispersers increased over time. Second, geographic variation in reporting rates can influence interpretation of dispersal patterns. Reporting rates are thought to be consistently high in British Colum-

bia waters but have varied widely over time and location within Alaska waters (Hanselman et al., 2015); they have not been estimated for the U.S. West Coast (California, Oregon, and Washington). Our results may have been biased toward higher or lower dispersal than indicated by tag returns, depending on spatial differences in reporting rates. Third, geographic or temporal variation in fishing effort can bias the interpretation of migration patterns. As noted above, the recently increased effort in deep slope waters off Oregon appeared to impact the temporal likelihood of recaptures from the deeper sites of tagging set 2. However, recaptures in a nearly continuous contour along the slope from northern California to the Aleutian Islands reflect the geographic continuity of fishing effort throughout sablefish habitat. Finally, the tagging process in itself can impact fish biology. McFarlane and Beamish (1990) found that the presence of a Floy tag reduced growth and delayed maturity in sablefish. In our study, most of our comparisons were between different groups of tagged fish—comparisons that could be assumed to be valid if all were impacted similarly by the presence of a tag. Our calculated growth rates may have been underestimates, however.

Additional caveats concern the sampling design of our study. Fish were not collected and tagged from a broad region of depths between zones 2 and 3 (depths of 650–1110 m). It is possible that some of our conclusions regarding depth-related movements could be modified if these depths had been included in sampling. In addition, with the growth model that we developed, there was the assumption of a smooth transition of growth rates from shallower to deeper habitats. It is possible that the decline in growth with depth instead follows a step function that matches transitions in habitat, such as those transitions associated with the OMZ or other parameters of habitat quality.

Implications for management

Our results concur with those of prior comparisons of northern and southern stocks of sablefish, particularly in the strong 'resident' behavior of Oregon fish. However, fish that did disperse often travelled thousands of kilometers away from Oregon, primarily into Gulf of Alaska waters. Within the northern stock there is extensive movement throughout the Gulf of Alaska and Bering Sea (summarized by Echave et al., 2013, and Hanselman et al., 2015), but there is more limited migration to waters within the range of the southern stock. Thus, overall, the 2 stocks are geographically distinct, which supports the current stock separation for management, but there is sufficient interchange to prevent genetic distinction. Because tagging studies to date have resulted in removal of fish from the population, movement patterns of individuals over their lifetimes and the extent to which dispersers return to the location of tagging are unknown. Likewise, movement patterns are unknown for the many fish that were caught near their tagging location after many years at large. It might be hypothesized that the northward dispersers in this study were northern fish that had made a temporary excursion to the south, but the dispersers tended to be smaller in size at tagging, suggesting they were spawned in Oregon. Future studies with archival and satellite tags (Echave et al., 2013) can provide insight into the extent to which fish make repeated movements from one region of the population to another. If the movement is a one-time event, then those fish will be lost to their respective stocks.

The recaptures from tagging set 2 indicated that warm surface temperatures may increase discard mortality rates for small fish. This outcome may be important in a management context because smaller fish are more likely to be discarded at sea in favor of retention of more valuable larger fish. Our results are likely to reflect a best case scenario, in which fish were captured by pots, carefully handled and released, and exposed to relatively moderate temperatures even in the high treatment (15.3–17.8°C). Surface temperatures during extreme El Niño–Southern Oscillation conditions as well as those predicted with climate change will likely exceed those of our study. Effects of capture depth on discard mortality rates were confounded in our study with fishing effort. The reduced recapture rates from depth zone 3 in relation to depth zone 2 may have largely reflected the much lower fishing effort within depth zone 3, particularly during the initial post-tagging period. A more evenly balanced effort to recover tagged fish would be necessary to discern a depth effect on discard mortality.

The potential trade-off between growth and longevity along the slope depth gradient may be altered by future climate change effects, such as predicted increases in hypoxic conditions in coastal habitats and shoaling of the oxygen minimum layer (Pierce et al., 2012; Gilly et al., 2013). The capacity of sablefish to tolerate low oxygen conditions may benefit their future survival but at an unknown cost to individual growth rates. Low exploitation rates in very deep slope habitats may help to provide a spatial refuge, allowing accrual of the ecological benefits of a long life span.

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Trophic segregation of mixed schools of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in the eastern tropical Pacific Ocean

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Abstract—One of the major challenges in trophic ecology is to understand how organisms interact with each other and to apply this knowledge to the management of populations, communities and ecosystems. Our goal was to examine fine-scale variability in the feeding habits and trophic position of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught together in mixed schools by purse seine to examine the null hypothesis that the association between these 2 tuna species is not related to trophic interactions. In total, 439 yellowfin tuna and 216 skipjack tuna were collected in 3 different areas in the eastern tropical Pacific Ocean during 2005. The stomachs of both tuna species contained prey at different stages of digestion, which indicated intermittent feeding throughout the course of the day. Yellowfin tuna consumed mainly epipelagic crustaceans and mesopelagic squids, whereas epipelagic euphausiids and epipelagic flyingfish were the most abundant prey species in the stomach contents of skipjack tuna. Our results suggested that both tuna species employed an opportunistic predation strategy, but significant dietary differences showed that they occupy different trophic levels, and that there is no food competition between yellowfin and skipjack tunas in the eastern tropical Pacific Ocean.

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The eastern tropical Pacific Ocean (ETPO) is one of the most productive oceanic provinces on the planet (Picaut, 1985; Fiedler et al., 1991; Pennington et al., 2006). The tuna fishery in the ETPO is one of the most important in the world; the 2012 annual catches of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) exceeded 209,000 and 271,000 metric tons, respectively (IATTC[1]).

Yellowfin and skipjack tunas are schooling species that are frequently found together in large aggregations (Scott et al., 2012); in the ETPO they are often co-occurring and captured by purse-seine near the sea surface. Despite intensive research on these 2 tuna species, the association between them remains unexplained. The best documented and understood association between large marine organisms in the ETPO is that between yellowfin tuna and dolphins (Stuntz[2]; Scott and Cattanach, 1998). The tuna–dolphin association appears to be a strategy to reduce the risk of predation for one or both species (Scott et al., 2012).

Associations among marine organisms can result in increased feeding success of one or both of the associated species (Nikolsky, 1963). Yellowfin and skipjack tunas require large amounts of energy to sustain themselves (Olson and Boggs, 1986;

[1] IATTC (Inter-American Tropical Tuna Commission). 2014. Tunas and billfishes in the eastern Pacific Ocean in 2013. Inter-Am. Trop. Tuna Comm., Fish. Status Rep. 12, 177 p. [Available from website.]

[2] Stuntz, W. E. 1981. The tuna-dolphin bond: a discussion of current hypotheses. NOAA Southwest Fish. Cent., Admin. Rep. LJ-81-19, 9 p.

Korsmeyer and Dewar, 2001), and consequently previous authors have suggested that food acquisition is one factor that could explain the association of these 2 tuna species (Sund et al., 1981; Petit, 1991). The diets of yellowfin and skipjack tunas in the ETPO have been described individually (Galván-Magaña, 1988; Román-Reyes, 2000; Olson et al., 2014) with notable intraspecific differences related to size class and time of capture (yellowfin tuna: Olson et al., 2014; skipjack tuna: IATTC[1]). The diets of co-occurring yellowfin and skipjack tunas in the northern ETPO were evaluated by Alverson (1963), and he found only a minor diet overlap owing to the consumption of pelagic red crabs (*Pleuroncodes planipes*) by both species. There is, therefore, a scarcity of information regarding whether competitive trophic interactions play a role in the association between yellowfin and skipjack tunas throughout the entire ETPO. Apart from documenting diet overlap and potential competition, diet studies of predatory fishes also provide valuable information on ingested prey and their spatial and temporal variation in abundance and biomass. Understanding interactions in the food web is a prerequisite for gaining insight into the role of predators, commercial fisheries, and environmental effects on ecosystem structure and dynamics. Prey species are often the central key link in such interactions (Galván-Magaña, 1999; Olson and Watters, 2003; Griffiths et al., 2013).

The goals of our study were 1) to analyze the diets of associated yellowfin and skipjack tunas caught in the ETPO, and 2) to examine diet variability in terms of the area, season, capture time of day, and tuna size class and sex in order to assess the hypothesis that competitive trophic interactions form the basis for the association between these 2 tuna species. Our data provide important information on the feeding strategies of yellowfin and skipjack tunas on mid-trophic-level communities at various spatiotemporal scales in the pelagic ETPO.

Materials and methods

The study area was located in the ETPO between 35° and 5°N, and from 140°W to the coastline (Fig. 1). This area is characterized by a well-developed, relatively shallow thermocline, generally less than 100 m deep and is influenced by 6 major surface currents and 4 subsurface currents (Kessler, 2006). Zone 1 is influenced partially by the California Current. Zone 3 is influenced by the North Equatorial Current, and both zones 2 and 3 are influenced by the North Equatorial Counter Current, and the north and south subsurface Counter Current (Lavin et al., 1997).

Samples of yellowfin and skipjack tunas were collected simultaneously from 25 purse-seine sets during 15 trips by observers from the Inter-American Tropical Tuna Commission, between January through November 2005. In the ETPO, the tuna fleet uses 3 types of capture methods: sets associated with floating objects, sets associated with dolphins, and sets associated with free-swimming schools of tuna that are not associated with floating objects or with larger marine species. The tunas were identified, the capture location, date, time of day (morning, afternoon, or evening), fork length (FL), and sex of each specimen were recorded, and the stomach contents were collected and immediately frozen.

The stomach analyses were conducted at the Centro Interdisciplinario de Ciencias Marinas in La Paz, Mexico. In the laboratory, we thawed the stomach contents and categorized the digestive state of the prey species according to the digestive levels described by Galvan-Magaña (1988) who assigned 4 digestive levels: 1=food includes recently consumed items; 2=food items with little to no skin remaining; 3=presence of fish skeletons; and 4=presence of hard structures like fish otoliths, crustacean remains, and cephalopod beaks.

For prey items (fish, crustaceans, and cephalopods) at digestive level 1, we used identification keys by Allen and Robertson (1994), Fischer et al. (1995), and Thomson et al. (2000); whereas for prey items at digestive levels 2 and 3, we used the taxonomic key by Clothier (1950), which is based on vertebral characteristics (e.g., number, position, and form of the vertebrae). Finally, prey items at digestion level 4 were identified by using keys by Fitch and Brownell (1968) for fish species, Brusca (1980) for crustaceans, and Wolff (1984) and Clarke (1986) for cephalopods.

Once the prey items were identified, the data were stratified by area (based on Galván-Magaña, 1999), month, time of capture, sex, and size class. Size classes were divided at 85 cm FL for yellowfin tuna, with small defined as 1–85 cm FL and large defined as >85 cm FL, (Schaefer, 1998); and at 50 cm FL for skipjack tuna, with small defined as 1–50 cm FL and large defined as >50 cm FL (IATTC[3]). Capture time intervals were morning (0900–1059), afternoon (1100–1359), and evening (1400–1600).

We used the program EstimateS (Colwell, 2006) to construct cumulative prey curves to determine whether the number of stomachs collected were sufficient to represent the diet of both yellowfin and skipjack tunas (Ferry and Cailliet, 1996). The cumulative curves were generated by randomizing the species richness and abundance data (100 times) for the total number of stomachs to obtain cumulative Shannon-Wiener diversity values. Then, we calculated the coefficient of variation (CV) of the diversity values as an indicator of the degree of variability of the diet. CVs <0.05 were considered adequate for the representation of the trophic spectrum of yellowfin and skipjack tunas (Steel and Torrie, 1992). Finally, cumulative diversity and CV values were plotted in relation to the number of stomachs analyzed.

[3] IATTC (Inter-American Tropical Tuna Commission). 2002. Annual report of the Inter-American Tropical Tuna Commission 2000, 171 p. IATTC, La Jolla, CA. [Available from website.]

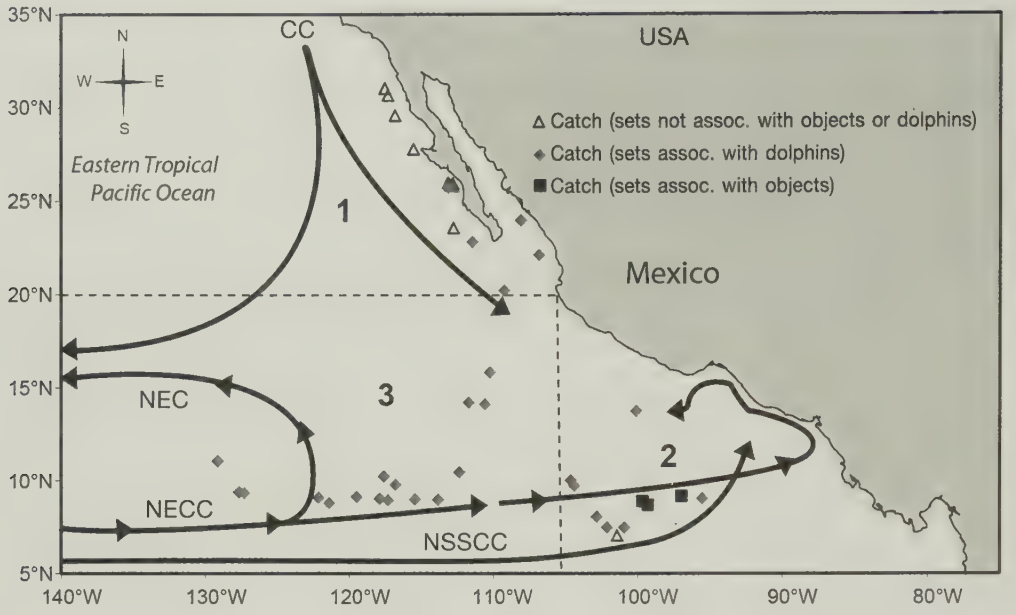

Figure 1

Map of zones (1, 2, and 3) in the eastern tropical Pacific Ocean fished by the Mexican tuna fleet. The zones are based on trophic relationships between pelagic top predators according to Galván-Magaña (1999), and on the subsurface currents that influence the zones: California Current (CC), North Equatorial Current (NEC), North Equatorial Counter Current (NECC), North and South subsurface Counter Current (NSSCC), according to Lavin et al. (1997). Squares, triangles, and diamonds indicate locations where tunas were caught in 2005 in sets associated (assoc.) with floating objects, in sets not associated with floating objects or dolphins), and in sets associated with dolphins, respectively.

The diet data for both species were analyzed as mean proportions by number (%MN) and weight (%MW) for individual fish, then averaged for each prey type, and multiplied by 100 (Chipps and Garvey, 2007). Also, the index of relative importance index (IRI) was calculated with the formula described by Pinkas et al. (1971) and modified as a percentage (Cortés, 1997):

$$IRI = (\%N + \%W) \times \%FO, \quad (1)$$

where %N and %W = the number and wet weight of each food item as percentages, respectively; and
%FO = the percentage frequency of occurrence (presence–absence) of each food item in all stomachs that contained food.

The diet breadth (B_i) of yellowfin and skipjack tunas was evaluated with the Levin´s standardized index by sex, size class, month, and time interval of capture (Krebs, 1999). Index values ranged from 0 to 1; low values (<0.6) indicated specialist diets and higher values (≥0.6) indicated generalist diets (Labropoulou and Eleftheriou, 1997).

$$B_i = \frac{1}{(n-1)}\left(\frac{1}{(\sum_{ji}^{P^2}} - 1\right), \quad (2)$$

where B_i = Levin's index for predator I;
ΣP^2_{ji} = the numerical proportion of the jth prey item in predator i's diet; and
n = the number of prey categories.

The trophic level (TL_i) of yellowfin and skipjack tunas based on stomach contents was calculated with the equation proposed by Christensen and Pauly (1992):

$$TL_i = 1 + \left(\sum_{j=1}^{n} DC_{ji}\right)\left(TL_j\right), \quad (3)$$

where TL_i = the trophic level of predator species i;
DC_{ji} = the diet composition in weight, in terms of the prey proportion j in the predator diet i;
TL_j = the trophic level of all prey species j; and
n = the number of prey groups in the diet.

The TL_j for fish prey species (Table 1) were obtained from FishBase (Froese and Pauly[4]), and those for cephalopods and crustaceans were obtained from Cortés (1999). We calculated the mean and standard deviation (SD) to represent the variability of the individual TL_i values.

[4] Froese, R., and D. Pauly (eds.). 2006. FishBase. World Wide Web electronic publication. [Available from website, accessed November 2006.]

Table 1

Trophic levels of prey species (TL_j) present in the diets of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in the eastern tropical Pacific Ocean in 2005. The values of TL_j for each prey species were obtained in the references cited in the table and provided below

Prey item		TL_j	References
Cephalopoda			
Teuthoidea		3.20	Cortés, 1999[1]
Lepidoteuthidae	*Pholidoteuthis boschmai*	3.20	Cortés, 1999[1]
Loliginidae	*Lolliguncula (Loliolopsis) diomedeae*	3.20	Cortés, 1999[1]
Onychoteuthidae	*Onychoteuthis banksii*	3.20	Cortés, 1999[1]
Ommastrephidae	*Dosidicus gigas*	3.20	Cortés, 1999[1]
	Sthenoteuthis oualaniensis	3.20	Cortés, 1999[1]
Thysanoteuthidae	*Thysanoteuthis rhombus*	3.20	Cortés, 1999[1]
Mastigoteuthidae	*Mastigoteuthis dentata*	3.20	Cortés, 1999[1]
Octopoda			
Bolitaenidae	*Japetella diaphana*	3.20	Cortés, 1999[1]
Argonautidae	*Argonauta* spp.	3.20	Cortés, 1999[1]
Octopodidae	*Octopus rubescens*	3.20	Cortés, 1999[1]
Crustacea			
Squillidae	Squillid mantis shrimps	2.52	Cortés, 1999[1]
Euphausiidae	*Nyctiphanes simplex*	2.52	Cortés, 1999[1]
Galatheidae	*Pleuroncodes planipes*	2.52	Cortés, 1999[1]
Penaeidae	Penaeid shrimps	2.52	Cortés, 1999[1]
Teleostei			
Clupeidae	*Harengula thrissina*	3.10	Whitehead and Rodriguez-Sánchez, 1995[2]
Phosichthyidae	*Vinciguerria lucetia*	3.00	Lipskaya, 1985[3]
Hemiramphidae	*Oxyporhamphus micropterus*	3.10	Lipskaya 1987[4]
Exocoetidae	*Exocoetus* spp.	3.10	Lipskaya 1987[4]
	Exocoetus monocirrhus	3.10	Gorelova 1980[5]
	Exocoetus volitans	3.10	Lipskaya 1987[4]
	Hirundichthys spp.	3.10	Lipskaya 1987[4]
Carangidae	Jacks	4.20	Cortés 1999[1]
	Seriola lalandi	4.10	Craig 1960[6]
Coryphaenidae	*Coryphaena hippurus*	4.50	Palko et al. 1982[7]
Bramidae	*Brama* spp.	4.40	Watanabe et al. 2006[8]
Gempylidae	*Gempylus* spp.	4.35	Nakamura 1995[9]
Scombridae	*Auxis* spp.	4.34	Blaber et al. 1990[10]
Nomeidae	*Cubiceps pauciradiatus*	3.50	Gorelova et al. 1994[11]
Balistidae	*Balistes polylepis*	3.34	Grove and Lavenberg 1997[12]
Ostraciidae	*Lactoria diaphana*	3.50	Grove and Lavenberg 1997[12]

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Table 2

Fork lengths, measured in centimeters, of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in mixed schools in the eastern tropical Pacific Ocean in 2005, with standard deviations (SDs) given in parentheses after the means. No.=number of samples.

	Zone 1				Zone 2				Zone 3			
	No.	Min	Max	Mean (SD)	No.	Min	Max	Mean (SD)	No.	Min	Max	Mean (SD)
Yellowfin tuna	124	39.9	112.1	69.8 (12.8)	129	47.0	129.3	80.8 (17.8)	186	48.9	130.0	79.5 (19.0)
Skipjack tuna	104	39.2	67.5	52.5 (4.6)	79	41.0	84.5	57.1 (8.1)	33	40.8	69.4	50.8 (8.5)

An analysis of similarities (ANOSIM) and the similarity percentage (SIMPER) analysis were carried out to evaluate the differences in diet within and between each tuna species and to establish the contribution of each prey item, respectively, with PRIMER, vers. 6.1.6 (PRIMER-E, Auckland, New Zealand). For both analyses, we used permutation–randomization methods based on the Bray-Curtis measure of similarity, also termed "the percentage difference," which is related to the mean character difference (Clarke and Warwick, 2001). The Bray–Curtis method operates at the species level, and therefore the mean similarity between groups (e.g., between males and females) can be obtained for each tuna species.

Results from ANOSIM are represented on an R scale from +1 to −1. An R value of +1 indicates that all the most similar samples are within the same groups. An R value of 0 occurs if the high and low similarities are perfectly mixed and bear no relationship to the group and indicate a completely random distribution within the group. An R value of −1 indicates that the most similar samples are all outside of the groups. Values from ANOSIM between 0.2 and 1 with significance set at $P<0.05$ indicate that the null hypothesis can be rejected and the tuna species would have significantly different diets (Clarke and Warwick, 2001). The SIMPER analysis breaks down the percentage contribution of each species to the observed similarity (or dissimilarity) between samples. Diet comparisons between yellowfin tuna and skipjack tuna were evaluated by comparing individuals captured in the same set within each area.

Results

Cumulative curves for size classes and prey species

We sampled 439 yellowfin tuna and 216 skipjack tuna from mixed schools. Yellowfin tuna were the largest (mean FL) in zone 2 and the smallest in zone 1. Skipjack tuna were similar in mean FL in all 3 zones (Table 2). For all the yellowfin tuna samples, 381 stomachs (87%) contained food, and 58 (13%) were empty; whereas, for all the skipjack tuna samples, 109 stomachs (51%) contained food, and 107 (49%) were empty (Table 3).

Out of a total of 25 sets, yellowfin tuna occurred in all sets and skipjack tuna occurred in only 8 sets. For yellowfin tuna, 124 stomachs with food were obtained from 9 sets in zone 1, 91 were obtained from 7 sets in zone 2, and 166 were obtained from 9 sets in zone 3. For skipjack tuna, 75 stomachs with food were obtained from 5 sets in zone 1, 22 were obtained from 2 sets in zone 2, and 12 were obtained from 1 set in zone 3. Cumulative curves for the prey species for each zone showed that a sufficient number of stomachs were analyzed to characterize the diet of both species (Fig. 2), with the CVs <0.05 in all areas.

Digestive state of prey species

The state of digestion of the prey of both yellowfin and skipjack tunas varied widely in each sample zone. In zone 1, both tuna species had the highest number of prey species in digestive level 2. In zone 2, prey species in digestion level 4 were the most common whereas in zone 3, prey species were most often at digestive level 3 (Table 4).

Diet composition in zone 1

Yellowfin tuna prey items comprised 21 taxa (9 cephalopods, 2 crustaceans, and 10 fish species). The %MN and %MW indices indicated that the most important prey items were the pelagic red crab (48.9%; 54.2%), the jumbo squid (*Dosidicus gigas*) (20.7%; 16.6%), and the bigeye cigarfish (*Cubiceps pauciradiatus*) (13.4%; 13.9%), respectively. According to the IRI, pelagic red crab (61.1%) and jumbo squid (28.7%) were the most important components in the diet (Table 5). The diversity index was 1.4 and B_i was 0.1. The trophic level of the stomach contents was estimated at 3.9 (SD 0.4). The ANOSIM test indicated a similar diet composition by sex (R=0.009), and differences among size classes (R=0.300, P=0.04; small individuals primarily consumed jumbo squid and pelagic red crabs; whereas large individuals primarily consumed *Cubiceps* spp.), months (R=0.360, P=0.01; in February individuals primarily consumed *Cubiceps* spp., jumbo squid, and

Table 3

Summary description of samples of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in 2005 in the eastern tropical Pacific Ocean and used for stomach contents analyses. The size classes for yellowfin tuna were small (S), 1–85 cm in fork length (FL), and large (L), >85 cm FL. The size classes for skipjack tuna were small (S) 1–50 cm FL, and large (L), 50 cm FL). Capture times were morning (0900–1059 h), afternoon (1100–1359 h), and evening (1500–1600 h). TS=total stomachs; SWC=stomachs with content; n/d=no data.

			Number of samples		
Species	Category	Group	Zone 1 TS (SWC)	Zone 2 TS (SWC)	Zone 3 TS (SWC)
Thunnus albacares	Males	S	64 (64)	45 (30)	58 (52)
		L	6 (6)	15 (12)	24 (21)
	Females	S	48 (48)	50 (33)	71 (63)
		L	6 (6)	19 (16)	33 (30)
	Month	Jan.	n/d	89 (51)	n/d
		Feb.	40 (40)	25 (25)	40 (37)
		Aug.	45 (45)	n/d	n/d
		Sep.	24 (24)	n/d	20 (19)
		Oct.	n/d	15 (15)	126 (110)
		Nov.	15 (15)	n/d	n/d
	Capture time	Morning	22 (22)	24 (20)	60 (55)
		Afternoon	55 (55)	30 (28)	49 (45)
		Evening	47 (47)	75 (43)	77 (66)
Katsuwonus pelamis	Males	S	1 (1)	4 (4)	7 (3)
		L	43 (29)	34 (6)	9 (3)
	Females	S	12 (10)	6 (5)	10 (4)
		L	48 (35)	35 (7)	7 (2)
	Month	Jan.	n/d	30 (10)	n/d
		Feb.	n/d	49 (12)	19 (5)
		Aug.	94 (65)	n/d	n/d
		Sep.	n/d	n/d	3 (3)
		Oct.	10 (10)	n/d	11 (4)
		Nov.	n/d	n/d	n/d
	Capture time	Morning	25 (20)	30 (8)	4 (3)
		Afternoon	54 (35)	15 (6)	6 (3)
		Evening	25 (20)	34 (10)	23 (6)

pelagic red crab, in August they primarily consumed jumbo squid and pelagic red crab, in September they primarily consumed pelagic red crab and *Auxis* spp., in November they primarily consumed the Panama lightfish [*Vinciguerria lucetia*]), and capture times (R=0.310, P=0.01; in the morning individuals primarily consumed *Cubiceps* spp., in the afternoon they primarily consumed jumbo squid and pelagic red crab, and in the evening they primarily consumed Panama lightfish, jumbo squid, and pelagic red crab) (Fig. 3).

Skipjack tuna prey items comprised 5 taxa (2 cephalopods, 2 crustaceans and 1 fish species). The %MN and %MW indices indicated that the most important prey items were a krill species, *Nyctiphanes simplex* (60.0%; 60.0%), pelagic red crab (20.0%; 20.0%), and tropical two-wing flyingfish (*Exocoetus volitans*) (12.0%; 12.0%), respectively. According to the IRI, *N. simplex* (98.6%) and *Argonauta* spp. (1.3%) were the most important components in the diet (Table 5). The diversity index was 1.1 and the B_i was 0.003. The trophic level of the stomach contents was estimated at 3.5 (SD 0.4). The ANOSIM test indicated a similar diet composition for the sexes (R=0.007), size class (R=0.094), months (R=0.018), and capture times (R=0.099).

Diet composition in zone 2

Yellowfin tuna prey items comprised 19 taxa (7 cephalopods, 1 crustaceans, and 11 fish species). Based on the %MN and %MW indices, the most important prey items were *Argonauta* spp. (33.1%; 20.6%), jumbo squid (27.9%; 27.7%), and *Auxis* spp. (9.5%; 19.9%), respectively. According to the IRI, jumbo squid (55.3%), *Argonauta* spp. (30.4%), and *Auxis* spp. (11.2%) were the most important components in the diet (Table 6). The diversity index was 1.3 and the B_i was 0.1. The trophic level of the stomach contents was estimated at 4.7 (SD 0.2). The ANOSIM test indicated a similar

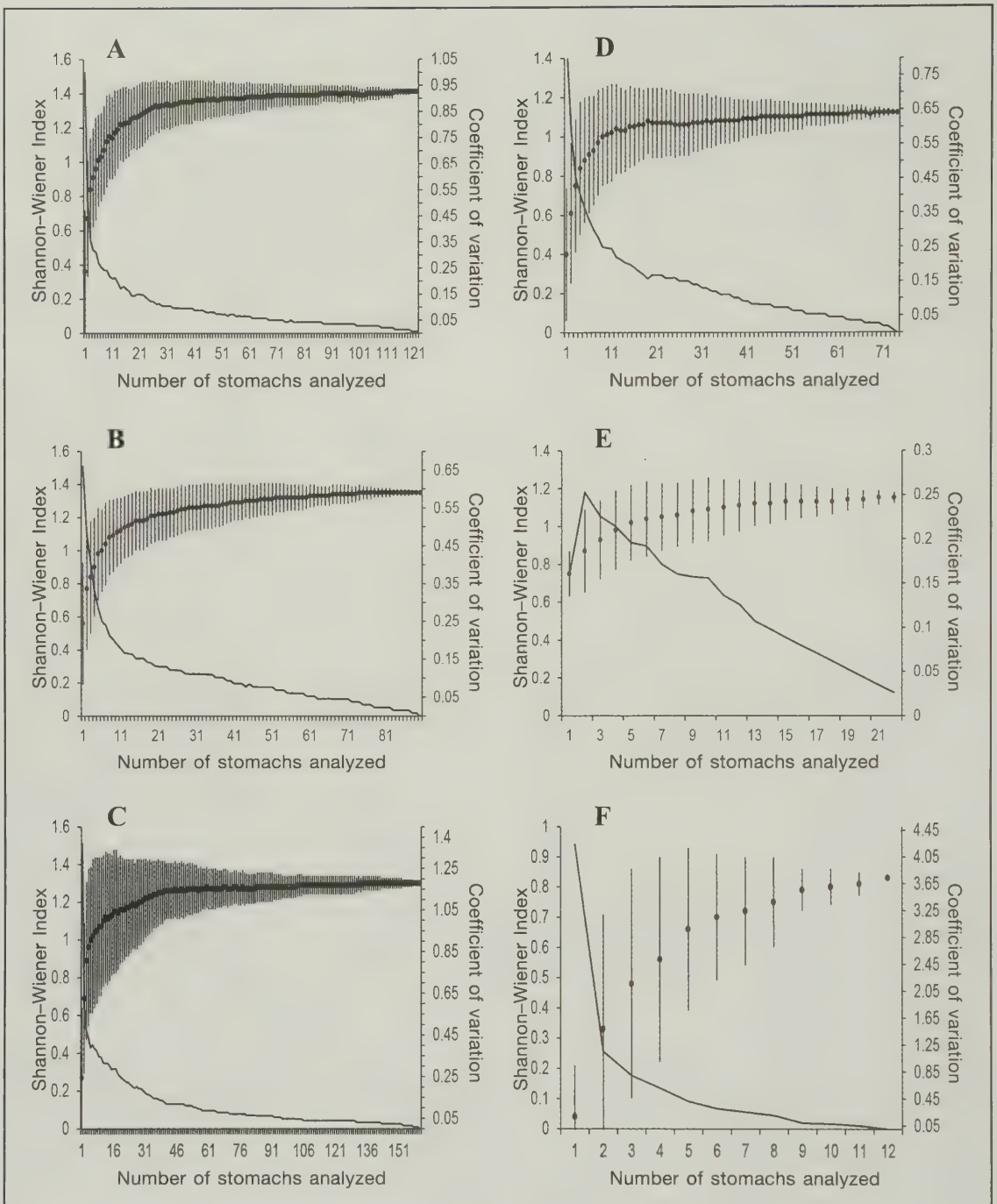

Figure 2

Randomized cumulative prey curves generated by using the Shannon–Wiener diversity index for yellowfin tuna (*Thunnus albacares*) in (**A**) zone 1, (**B**) zone 2, and (**C**) zone 3 and for skipjack tuna (*Katsuwonus pelamis*) in (**D**) zone 1, (**E**) zone 2, and (**F**) zone 3. The black lines indicate coefficients of variation. The vertical black lines indicate standard deviations.

diet composition among sexes (R=0.017), size classes (R=0.062), and capture times (R=0.020), and diet differences among months of capture (R=0.400, P=0.01; January=*Argonauta* spp., *Auxis* spp., jumbo squid; February=jumbo squid; October=*Auxis* spp., smallwing flyingfish [*Oxyporhamphus micropterus*], Fig. 4).

Skipjack tuna prey items comprised 7 taxa (1 cephalopod and 6 fishes). Based on the %MN and %MW indices, the most important prey items were tropical two-wing flyingfish (79.5%; 79.8 %) and smallwing flyingfish (4.4%; 5.3%), respectively (Table 6). According to the IRI, tropical two-wing flyingfish (96.2%) and smallwing

Table 4

Number of prey items present in the diet of yellowfin tuna (YT; *Thunnus albacares*) and skipjack tuna (ST; *Katsuwonus pelamis*) caught in 2005 in fishng zones 1–3 in the eastern tropical Pacific Ocean, by digestive state (DS), geographic zone, capture time (morning [M], afternoon [A], and evening [E]) and category of prey species (fish [F], cephalopod [C], and crustacean [Cr]). DS level 1= food includes recently consumed items; DS level 2=food items with little to no skin remaining; 3 DS level=presence of fish skeletons; and DS level 4=presence of hard structures like fish otoliths, crustacean remains, and cephalopod beaks.

			Zone 1				Zone 2				Zone 3			
Capture time	Predator species	Prey species	DS 1	DS 2	DS 3	DS 4	DS 1	DS 2	DS 3	DS 4	DS 1	DS 2	DS 3	DS 4
M	YT	F	0	9	159	1	0	2	2	0	0	6	103	16
		C	0	0	0	3	0	0	1	79	0	29	21	235
		Cr	2	2	0	0	0	0	0	0	35	637	563	0
	ST	F	0	0	17	1	0	0	0	0	0	0	0	0
		C	0	0	0	1	0	0	0	0	0	0	0	0
		Cr.	0	4744	1196	0	0	0	0	0	0	0	0	0
A	YT	F	0	86	423	0	0	1	9	30	0	0	36	0
		C	56	175	102	384	0	0	17	475	0	1	0	38
		Cr	218	1498	329	0	0	0	0	1	0	0	0	0
	ST	F	0	0	7	0	0	0	26	3	0	0	0	0
		C	0	0	0	5	0	0	0	1	0	0	0	0
		Cr	2227	32,251	2159	0	0	0	0	1	0	0	0	0
E	YT	F	0	4	948	1	0	6	204	14	0	7	1229	2
		C	0	216	0	641	0	111	29	626	0	0	7	160
		Cr	66	545	362	1	0	0	1	0	0	26	268	0
	ST	F	0	0	0	0	0	1	0	25	0	2	44	4
		C	0	0	0	3	0	0	0	0	0	2	0	0
		Cr	0	3628	120	0	0	0	0	0	0	0	0	0

flyingfish (2.49%) were the most important components in the diet. The diversity index was 1.1 and the B_i was 0.1. The trophic level of the stomach contents was estimated at 4.1 (SD 0.2). The ANOSIM test indicated a similar diet composition among sexes (R=0.009), size classes (R=0.020), months of capture (R=0.007), and capture times (R=0.120).

Diet composition in zone 3

Yellowfin tuna prey items comprised 23 taxa (8 cephalopods, 2 crustaceans and 13 fishes). The %MN and %MW indices indicated that the most important prey items were pelagic red crab (23.8%; 25.6%), *Argonauta* spp. (20.5%; 13.3%), and Panama lightfish (16.2%; 17.1%) respectively. According to the IRI, pelagic red crab (46.2%), Panama lightfish (24.7%), and *Auxis* spp. (17.4%) were the most important components of the diet (Table 7). The diversity index was 1.3 and the B_i was 0.1. The trophic level of the stomach contents was estimated at 4.5 (SD 0.4). The ANOSIM test indicated a similar diet composition among sexes (R=0.014), size classes (R=0.060), months of capture (R=0.120), and capture times (R=0.067).

Skipjack tuna prey items comprised 3 taxa (1 cephalopod and 2 fish species). The %MN and %MW indices indicated that the most important prey items were tropical two-wing flyingfish (66.7%; 66.8%) and Panama lightfish (29.2%; 25.0%) respectively. According to the IRI, tropical two-wing flyingfish (83.8%) and Panama lightfish (15.8%) were the most important components of the diet (Table 7). The diversity index was 0.8 and the B_i was 0.6. The trophic level of the stomach contents was estimated at 4.1 (SD 0.3). The ANOSIM test indicated a similar diet composition for sexes (R=0.098) and months of capture (R=0.180), and differences between size classes (R=0.212, P=0.04; small individuals primarily consumed tropical two-wing flyingfish, and large individuals primarily consumed Panama lightfish and tropical two-wing flyingfish) (Fig. 5). The ANOSIM test for capture times could not be performed because of the presence of empty stomachs.

Comparisons of diets

The ANOSIM showed differences in diet composition between yellowfin tuna and skipjack tuna in zone 1 (R=0.40, P=0.01), zone 2 (R=0.60, P=0.01), and zone 3 (R=0.25, P=0.01). A SIMPER analysis indicated changes in the contribution of each prey species between

Table 5

Summary of food categories in stomachs of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in 2005 in zone 1 of the eastern tropical Pacific Ocean, expressed as percentages of the mean proportion by number (%MN), mean proportion by weight (%MW), frequency of occurrence (%FO), and relative importance index (%IRI). x=not present in the diet; SWC=stomachs with content; TN=total number of prey examined; TW=total weight (in grams) of prey examined.

		Thunnus albacares (SWC=124)						*Katsuwonus pelamis* (SWC=75)					
Prey item		TN	%MN	TW	%MW	%FO	%IRI	TN	%MN	TW	%MW	%FO	%IRI
Cephalopoda													
Teuthoidea		6	0.93	26.0	1.10	1.62	0.01	x	x	x	x	x	x
Loliginidae	*Lolliguncula* (*Loliolopsis*) *diomedeae*	213	3.54	702.8	4.08	4.87	2.61	x	x	x	x	x	x
Ommastrephidae	*Dosidicus gigas*	1139	20.66	1122.9	16.59	54.47	28.26	8	6.66	0.1	6.66	6.66	0.01
	Sthenoteuthis oualaniensis	2	0.15	0.1	0.01	1.62	0.01	x	x	x	x	x	x
Thysanoteuthidae	*Thysanoteuthis rhombus*	3	0.14	0.1	0.01	2.43	0.01	x	x	x	x	x	x
Mastigoteuthidae	*Mastigoteuthis dentata*	4	0.20	0.1	0.01	2.43	0.01	x	x	x	x	x	x
Octopoda													
Bolitaenidae	*Japetella diaphana*	15	0.65	0.5	0.01	8.13	0.02	x	x	x	x	x	x
Argonautidae	*Argonauta* spp.	186	3.67	18.93	0.09	24.39	1.00	1	1.33	0.1	1.33	1.33	0.01
Octopodidae	*Octopus rubescens*	9	0.51	0.1	0.01	5.69	0.01	x	x	x	x	x	x
Crustacea													
Euphausiidae	*Nyctiphanes simplex*	x	x	x	x	x	x	46107	60.00	1750.4	60.00	60.00	98.60
Galatheidae	*Pleuroncodes planipes*	3021	48.89	1692.3	54.20	59.35	61.12	248	20.00	133.3	20.00	20.00	1.29
Penaeidae	Penaeid shrimps	2	0.01	1.1	0.01	0.81	0.01	x	x	x	x	x	x
Teleostei													
Clupeidae	*Harengula thrissina*	2	0.36	32.2	0.58	0.81	0.01	x	x	x	x	x	x
Phosichthyidae	*Vinciguerria lucetia*	1363	3.70	410.7	3.90	13.82	5.11	x	x	x	x	x	x
Exocoetidae	*Exocoetus* spp.	1	0.05	0.2	0.01	0.81	0.01	x	x	x	x	x	x
	Exocoetus volitans	x	x	x	x	x	x	25	12.00	8.5	12.00	12.00	0.05
Carangidae	*Seriola lalandi*	4	0.68	4.4	1.57	0.81	0.01	x	x	x	x	x	x
Coryphaenidae	*Coryphaena* spp.	1	0.22	5.5	0.90	0.81	0.01	x	x	x	x	x	x
Chaetodontidae	Chaetodontids	1	0.90	1.5	0.90	0.81	0.01	x	x	x	x	x	x
Scombridae	*Auxis* spp.	4	1.14	30.3	1.20	3.25	0.03	x	x	x	x	x	x
Nomeidae	*Cubiceps pauciradiatus*	253	13.36	338.4	13.94	0.81	1.81	x	x	x	x	x	x

tuna species. The prey species that contributed most to dissimilarity were *N. simplex* (53.7%) and pelagic red crab (21.9%), in zone 1; *Argonauta* spp. (28.2%), jumbo squid (25.0%), and tropical two-wing flyingfish (17.5%) in zone 2; Panama lightfish (24.5%), tropical two-wing flyingfish (22.1%), and pelagic red crab (18.2%) in zone 3 (Table 8).

Discussion

Digestive state of prey species

The variation in the degree of digestion of yellowfin tuna prey is related to the type of prey (fishes, cephalopods, and crustaceans) and the time of day when feeding occurs (Magnuson, 1969; Brill, 1987; Galvan-Magaña, 1988). Olson and Boggs (1986) found that squid soft tissue passed through the stomach of yellowfin tuna in 5–10 h, whereas the beak was the only cephalopod structure that persisted in the stomach because it is composed of digestion-resistant chitin. In contrast, the soft tissue of fishes passed through the stomach in about 6–18 h. Tunas are captured primarily during the day in the ETPO (Ortega-García et al., 1992). The low occurrence of prey found in digestive state 1 in the morning, but high in the afternoon and evening, indicated peak feeding activity in the afternoon and evening for both tuna species. This finding coincides with observations reported for different areas of the ETPO (Ortega-García et al., 1992; Román-Reyes, 2005). Because of the occurrence of prey in digestion state 2 and 3 (little fresh cephalopod tissue) in the afternoon and evening, we deduce that yellowfin and skipjack tunas actively feed on cephalopods at night and during early morning as they migrate to the surface (Olson and Boggs, 1986).

Also the presence of mesopelagic prey species in the diet of yellowfin and skipjack tunas may reflect the vertical migration habits of prey. Jumbo squid and

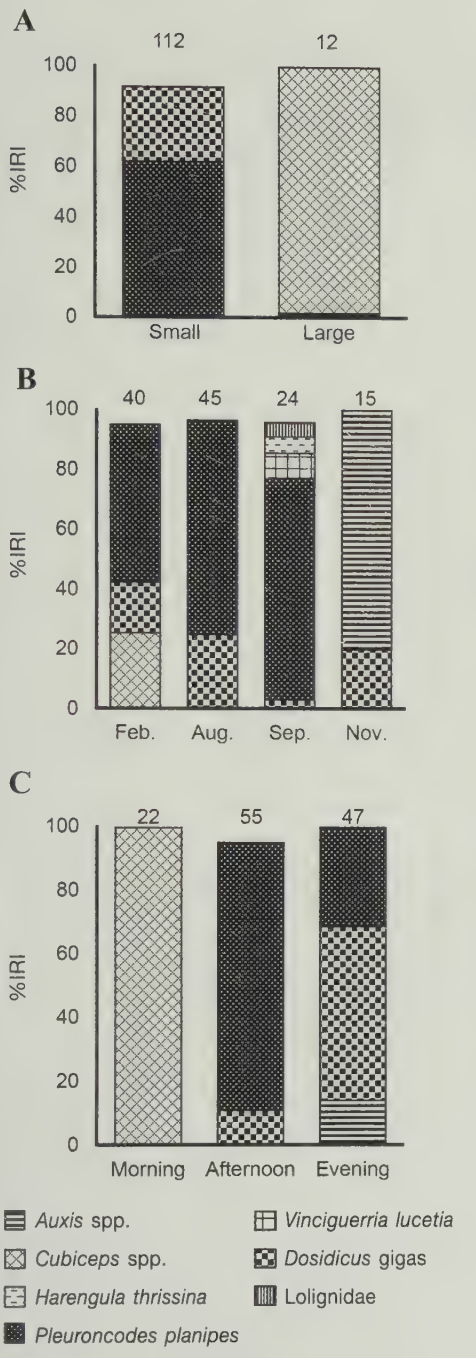

Figure 3

Variation in diet composition, determined with the relative importance index (%IRI), in relation to (**A**) size class (small, 1–85 cm in fork length [FL], and large, >85 cm FL), (**B**) months, and (**C**) capture time for yellowfin tuna (*Thunnus albacares*) caught in 2005 in zone 1 in the eastern tropical Pacific Ocean. The numeral above each bar indicates the number of stomachs with contents.

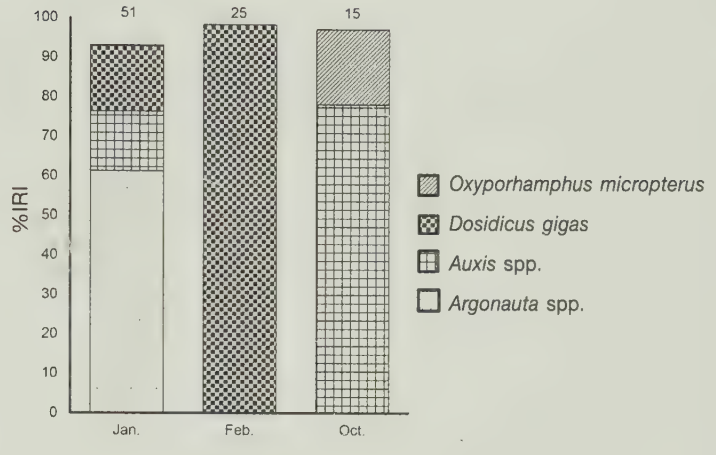

Figure 4

Variation in diet composition, determined with the relative importance index (%IRI), in relation to month of capture for yellowfin tuna (*Thunnus albacares*) caught in 2005 in the zone 2 in the eastern tropical Pacific Ocean. The numeral above each bar indicates the number of stomachs with content.

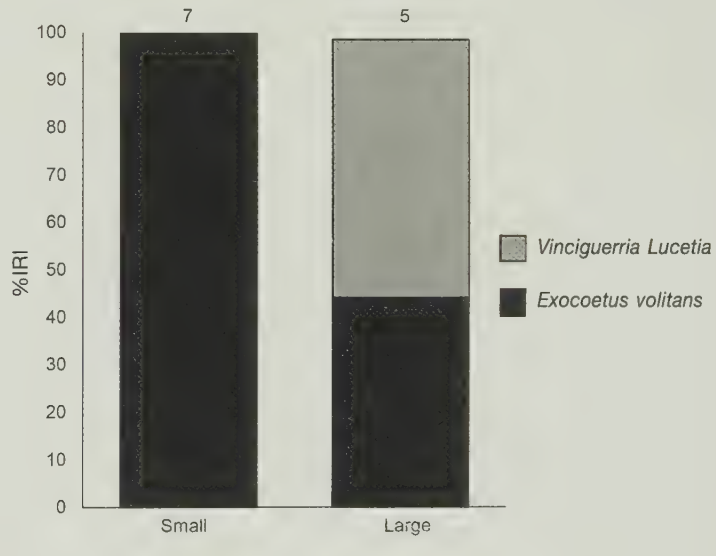

Figure 5

Variation in diet composition, determined with the relative importance index (%IRI), in relation to size class (small, 1–50 cm in fork length [FL], and large, >50 cm FL) of skipjack tuna (*Katsuwonus pelamis*) caught in 2005 in zone 3 in the eastern tropical Pacific Ocean. The numeral above each bar indicates the number of stomachs with content.

Panama lightfish make vertical migrations to the epipelagic area at night to feed (Olson and Boggs, 1986; Galván-Magaña, 1988). The presence of these prey species in the stomachs of yellowfin and skipjack tunas is likely the result of these movements into the epipelagic area where these tuna species forage.

Table 6

Summary of food categories in stomachs of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in 2005 in zone 2 of the eastern tropical Pacific Ocean, expressed as percentages of the mean proportion by number (%MN), mean proportion by weight (%MW), frequency of occurrence (%FO), and relative importance index (%IRI). x=not present in the diet; SWC=stomachs with content; TN=total number of prey examined; TW=total weight (in grams) of prey examined.

		Thunnus albacares (SWC=91)						*Katsuwonus pelamis* (SWC=22)					
Prey item		TN	%MN	TW	%MW	%FO	%IRI	TN	%MN	TW	%MW	%FO	%IRI
Cephalopoda													
Teuthoidea		1	8.98	0.1	2.89	12.63	0.01	x	x	x	x	x	x
Lepidoteuthidae	*Pholidoteuthis boschmai*	3	0.41	0.1	0.35	3.15	0.01	x	x	x	x	x	x
Ommastrephidae	*Dosidicus gigas*	612	27.95	2055.4	27.66	51.59	55.32	1	1.85	0.1	0.01	3.70	0.05
Thysanoteuthidae	*Thysanoteuthis rhombus*	11	0.685	1.1	1.77	9.47	0.01	x	x	x	x	x	x
Mastigoteuthidae	*Mastigoteuthis dentata*	20	0.87	0.1	0.97	8.42	0.12	x	x	x	x	x	x
Octopoda													
Bolitaenidae	*Japetella diaphana*	22	0.86	0.1	0.98	8.42	0.14	x	x	x	x	x	x
Argonautidae	*Argonauta* spp.	595	33.11	8.6	20.64	66.31	30.42	x	x	x	x	x	x
Crustacea													
Squillidae	Squillid mantis shrimps	1	0.14	1	0.55	1.05	0.01	1	1.85	0.1	0.01	3.70	0.05
Teleostei													
Clupeidae	*Harengula thrissina*	1	0.26	11	0.10	1.05	0.01	x	x	x	x	x	x
Phosichthyidae	*Vinciguerria lucetia*	160	6.39	55.9	8.47	8.42	1.17	1	3.70	0.2	3.70	3.70	0.06
Hemiramphidae	*Oxyporhamphus micropterus*	21	4.19	75.3	2.59	10.52	0.40	4	4.44	59.5	5.31	11.11	2.49
Exocoetidae	Exocoetids	2	0.05	30.6	1.12	2.10	0.02	1	1.85	2.5	3.70	3.70	0.08
	Exocoetus spp.	3	0.79	34.8	0.27	1.05	0.01	4	4.93	21.0	3.80	7.40	0.89
	Hirundichthys spp	x	x	x	x	x	x	1	1.85	13.0	3.70	3.70	0.19
	Exocoetus monocirrhus	1	0.02	0.1	0.02	1.05	0.01	x	x	x	x	x	x
	Exocoetus volitans	2	0.14	18.8	2.20	2.10	0.01	39	79.50	207.2	79.77	66.66	96.16
Carangidae	Jacks	1	1.46	14.35	2.86	1.05	0.01	x	x	x	x	x	x
Scombridae	Scombrids	1	4.20	13.0	6.67	1.05	0.01	x	x	x	x	x	x
	Auxis spp.	34	9.50	1725.3	19.89	21.05	11.20	x	x	x	x	x	x

Diet composition by zone

The diets of both tuna species are consistent with previous reports for the ETPO; however, we found fewer prey species in the fish stomachs than those of previous studies (Galván-Magaña, 1988; Román-Reyes, 2000). For yellowfin tuna, we recorded a total of 29 prey species, whereas Galván-Magaña (1988) reported a total of 53 prey species. For skipjack tuna, we recorded the occurrence of only 9 prey species, whereas Román-Reyes (2000) reported a total of 55 prey species in skipjack tuna stomachs. This variability in prey diversity may be associated with the number of stomachs analyzed; Galván-Magaña (1988) analyzed 1299 yellowfin tuna stomachs and Román-Reyes (2000) analyzed 611 stomachs of skipjack tuna. Despite the difference in the total number of prey species recorded, the most important prey have remained unchanged for both tuna species during the last 30 years in the ETPO. These include pelagic red crab, jumbo squid, and tropical two-wing flyingfish (Galván-Magaña, 1988; Román-Reyes, 2000; present study).

Crustaceans (primarily the pelagic red crab) were an important diet component by number, weight, and frequency of occurrence for both tuna species in zone 1, but only for yellowfin tuna in zone 3, which is in agreement with data reported by Alverson (1963). The pelagic red crab is a crustacean that has a pelagic juvenile phase, is present in high abundance at that phase, and is distributed vertically throughout the water column on the west coast of Baja California Sur, Mexico (zone 1). This region is influenced by the California Current during spring and summer. The abundance of the pelagic red crab in zone 3 may also be related to the intensity of the California Current (Lavin et al., 1997). Because the pelagic red crab is a passive swimmer, it can be transported to this zone by the California Current and therefore it becomes easy prey for several predators, including Panama hake (*Merluccius angustimanus*) (Balart and Castro-Aguirre, 1995), silky shark (*Carcharhinus falciformis*) (Cabrera-Chávez-Costa et al., 2010), and dolphinfish (*Coryphaena hippurus*) (Tripp-Valdez et al., 2010), in addition to yellowfin and skipjack tunas in both zones 1 and 3.

Table 7

Summary of food categories in stomachs of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in 2005 in Zone 3 of the eastern tropical Pacific Ocean, expressed as percentages of the mean proportion by number (%MN), mean proportion by weight (%MW), frequency of occurrence (%FO), and relative importance index (%IRI). x=not present in the diet; SWC=stomachs with content; TN=total number of prey examined; TW=total weight (in grams) of prey examined.

		Thunnus albacares (SWC=166)						*Katsuwonus pelamis* (SWC=12)					
Prey item		TN	%MN	TW	%MW	%FO	%IRI	TN	%MN	TW	%MW	%FO	%IRI
Cephalopoda													
Onychoteuthidae	*Onychoteuthis banksii*	27	0.90	0.1	0.72	3.10	0.07	x	x	x	x	x	x
Ommastrephidae	*Dosidicus gigas*	170	15.06	20.9	12.15	28.57	4.01	2	4.16	1.0	8.32	8.33	0.40
	Sthenoteuthis oualaniensis	8	1.37	0.5	1.70	3.10	0.01	x	x	x	x	x	x
Thysanoteuthidae	*Thysanoteuthis rhombus*	24	3.19	56.0	3.80	11.18	0.81	x	x	x	x	x	x
Mastigoteuthidae	*Mastigoteuthis dentata*	9	0.72	0.1	1.26	5.59	0.03	x	x	x	x	x	x
Octopoda													
Bolitaenidae	*Japetella diaphana*	16	3.02	0.1	3.26	8.69	0.09	x	x	x	x	x	x
Argonautidae	*Argonauta* spp.	235	20.52	3.6	13.31	39.13	6.59	x	x	x	x	x	x
Octopodidae	*Octopus rubescens*	6	0.19	0.1	0.33	2.48	0.01	x	x	x	x	x	x
Crustacea													
Galatheidae	*Pleuroncodes planipes*	1523	23.85	654.3	25.64	26.70	46.16	x	x	x	x	x	x
Squillidae	Squillid mantis shrimps	1	0.01	1.0	0.02	0.62	0.01	x	x	x	x	x	x
Teleostei													
Phosichthyidae	*Vinciguerria lucetia*	1330	16.18	435.5	17.14	18.01	24.71	25	29.16	3.1	25.00	33.33	15.78
Exocoetidae	*Hirundichthys* spp.	1	0.62	0.1	0.62	0.62	0.01	x	x	x	x	x	x
	Exocoetus monocirrhus	3	0.14	12.8	1.10	1.24	0.02	x	x	x	x	x	x
	Exocoetus volitans	x	x	x	x	x	x	25	66.66	3.0	66.67	66.66	83.81
Carangidae	Jacks	1	0.10	1.5	0.62	0.62	0.01	x	x	x	x	x	x
Coryphaenidae	*Coryphaena hippurus*	2	0.06	0.5	0.05	0.62	0.01	x	x	x	x	x	x
Bramidae	*Brama* spp.	2	0.64	2.8	0.82	1.24	0.01	x	x	x	x	x	x
Gempylidae	*Gempylus* spp.	1	0.02	0.2	0.40	0.62	0.01	x	x	x	x	x	x
Scombridae	Scombrids	1	0.10	0.1	0.60	0.62	0.01	x	x	x	x	x	x
	Auxis spp.	40	10.66	1179.4	13.37	14.28	17.38	x	x	x	x	x	x
Nomeidae	*Cubiceps pauciradiatus*	12	2.48	1.4	2.79	2.48	0.03	x	x	x	x	x	x
Balistidae	*Balistes polylepis*	1	0.02	5.1	0.17	0.62	0.01	x	x	x	x	x	x
Ostraciidae	*Lactoria diaphana*	1	0.05	0.5	0.61	0.62	0.01	x	x	x	x	x	x

In zone 2, yellowfin tuna preyed primarily on cephalopods, followed by fishes and crustaceans. This is in agreement with previous reports for this species in the ETPO (Alverson, 1963; Galván-Magaña, 1988, 1999; Román-Reyes, 2000, 2005; Olson et al., 2014). The main cephalopod prey items in the trophic spectrum of yellowfin tuna were jumbo squid of the family Ommastrephidae and *Argonauta* spp. of the family Argonautidae. Members of the Ommastrephidae family undertake nightly vertical migrations toward the surface to feed (Markaida-Aburto, 2001), whereas members of the genus *Argonauta* are mostly epipelagic species that feed primarily during the day (Nesis, 1977). These cephalopods were also present in skipjack tuna stomachs, but were not important to their overall diet. In contrast, Nakamura (1965) reported that cephalopods were an important dietary component for skipjack tuna in the southern Pacific Ocean. Our data show, however, that skipjack tuna preyed primarily on fishes and yellowfin tuna preyed primarily on cephalopods in zone 2, highlighting the dietary difference between these 2 predatory species within this geographic region.

In all 3 zones (1, 2, and 3), the most important prey species of yellowfin and skipjack tunas were those that form aggregations, such as the pelagic red crab, jumbo squid, tropical two-wing flyingfish, and Panama lightfish; this finding confirms those of Galván-Magaña (1988) and Alverson (1963). The prey consumed by yellowfin tuna were mainly epipelagic species (pelagic red crab in zones 1 and 3, and *Argonauta* spp. in zone 2), whereas mesopelagic species (e.g., jumbo squid in zones 1 and 2, and Panama lightfish in zone 3) were consumed in smaller amounts. Watanabe (1958) reported that yellowfin tuna fed mainly in the epipelagic zone, which is a direct result of its distribution in the water column (Eslava et al., 2003). The main prey items found in skipjack tuna stomachs were epipelagic species (e.g., *N. simplex*, *Auxis* spp., smallwing flyingfish, and tropical two-wing flyingfish), confirming the information in

Table 8

Results of the similarity of percentages analysis of taxa contributing to dissimilarity between yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in 2005 in zones 1, 2, and 3 of the eastern tropical Pacific Ocean, including average number of individuals (Av. abund), dissimilarity with standard deviation ratios (Diss/SD), and percentage of contribution to the overall Bray–Curtis similarity between assemblages of the 2 tuna species (Contrib%).

	K. pelamis Av. abund	*T. albacares* Av. abund	Diss/SD	Contrib%
Zone 1				
Average dissimilarity=95.10				
Prey species				
Nyctiphanes simplex	614.7	0.00	1.14	53.66
Pleuroncodes planipes	3.31	24.56	0.71	21.87
Dosidicus gigas	0.11	9.26	0.48	9.04
Vinciguerria lucetia	0.00	11.08	0.29	5.60
Zone 2				
Average dissimilarity=99.27				
Prey species				
Argonauta spp.	0.00	6.47	1.01	28.21
Dosidicus gigas	0.04	6.65	0.77	24.97
Exocoetus volitans	1.70	0.02	0.91	17.45
Vinciguerria lucetia	0.00	1.74	0.30	5.65
Zone 3				
Average dissimilarity=97.4				
Prey species				
Vinciguerria lucetia	2.08	8.26	0.71	24.50
Exocoetus volitans	2.08	0.00	0.84	22.12
Pleuroncodes planipes	0.00	9.46	0.53	18.22
Argonauta spp.	0.00	1.46	0.59	12.58

Román-Reyes (2000), whereas mesopelagic species (e.g., Panama lightfish) were consumed in zone 3.

The presence of mesopelagic prey species in the diet of yellowfin and skipjack tunas may reflect the vertical migration of prey species. Jumbo squid and Panama lightfish make vertical migrations to the epipelagic area at night to feed (Olson and Boggs, 1986; Galván-Magaña, 1988).

Comparison of diet between sexes and size classes

For both tuna species in all zones in our study, there were no significant differences in feeding between the sexes (ANOSIM values close to 0). Nakamura (1965), for skipjack tuna, and Alverson (1963), for yellowfin tuna, reported high diet similarity for both sexes, suggesting that males and females frequented the same areas. Between size classes, however, our data show dietary differences: in zone 1 for yellowfin tuna and in zone 3 for skipjack tuna. Olson and Boggs (1986) reported that the yellowfin tuna trophic spectrum (diet) in the ETPO depends on predator size—a result that we found in our data as well. Trophic level values were 3.9 for smaller fish and 4.5 for larger fish.

Changes in diet related to size can be attributed to differences in the energy requirements at distinct ontogenetic stages in the development of a fish (Olson and Galván-Magaña, 2002; Graham et al., 2007). For example, stage-specific dietary differences have been reported for skipjack tuna in other areas of the Pacific Ocean (Nakamura, 1965; Ankenbrandt, 1985). Our report of juvenile skipjack tuna feeding mainly on fishes (e.g., zone 3) is in agreement with that of Román-Reyes (2000), although the prey species differed. The main prey species of skipjack tuna in our study was the tropical two-wing flying fish, whereas Román-Reyes (2000) found the main prey species to be the mesopelagic fish *V. lucetia*. For yellowfin tuna, our data show that the juveniles fed on small abundant prey, such as pelagic red crab in zone 1, whereas adult yellowfin tuna fed on cephalopods or, as reported by Román-Reyes (2000), on fishes.

Diet variation of yellowfin and skipjack tunas is most likely to be related to the spatiotemporal distribution of the predators, and to the prey availability in different areas of the ETPO rather than to strict ontogenetic changes in predator size. Alverson (1963) mentioned that yellowfin tuna juveniles were usually

found in coastal areas where crustaceans are abundant, while adults were found in oceanic areas where cephalopods and fishes predominate. Thus, the high diet similarity between tuna of different sizes and the temporal (monthly, yearly) variation reported previously (Alverson, 1963; Nakamura, 1965; Román-Reyes, 2000) indicate that the consumption of distinct prey by organisms of different sizes may be more closely related to spatiotemporal segregation (oceanic in contrast with coastal segregation) of predators and prey than to size-related developmental shifts, such as a shift because of the added energy demands for reproduction.

Diet breadth

Values of B_i indicate that yellowfin and skipjack tunas are specialist predators; however, because the prey species were different in the 3 zones and form large aggregations (e.g., pelagic red crab and jumbo squid), these tunas can better be described as opportunistic predators, assuming that prey items are consumed in proportion to their abundance and availability in each zone. This conclusion is justified because tunas tend to feed often and on the most abundant prey (Olson and Boggs, 1986; Galván-Magaña, 1988). For example, in zones 1 and 3, the yellowfin tuna diet was dominated by pelagic red crab, which is abundant in upwelling areas of subtropical zones, generating large quantities of food that span several trophic levels (Alverson, 1963; Blackburn, 1969; Galván-Magaña, 1988; Cabrera-Chávez-Costa et al., 2010; Tripp-Valdez et al., 2010). In zone 2, yellowfin tuna consumed large quantities of jumbo squid, which is one of the main prey species in the ETPO. The jumbo squid lives in the mesopelagic zone but can also be found over the continental slope, mainly in upwelling areas rich in nutrients (Ehrhardt et al., 1986; Markaida-Aburto, 2001).

Trophic levels

Our calculations indicated that the prey of skipjack and yellowfin tunas have trophic level values between 3.5 and 4.1, and between 3.9 and 4.6, respectively. These estimates are consistent with trophic position estimates for the diet of yellowfin and skipjack tunas in the ETPO based on stomach contents and stable isotopes of nitrogen (Olson and Watters, 2003; Popp et al., 2007; Olson et al., 2010; Hunsicker et al., 2012). Interspecific comparison of trophic level shows that skipjack tuna feed lower in the food web than yellowfin tuna—a characteristic that is likely related to body size. Cortés (1999) mentioned that trophic levels of top predators increased with size, with larger predators having higher trophic levels than those of their smaller counterparts (Magnuson and Heitz, 1971). Also, several authors noted that trophic level may increase intraspecifically as fish grow (Cousins, 1980, Cohen et al., 1993) because they have access to different habitats (Graham et al., 2007). In addition, as predator size increases, prey capture efficiency also increases (Torres-Rojas et al., 2012). Our yellowfin tuna specimens were larger than our skipjack tuna specimens, and were thus able to capture a wider range of prey.

Comparisons of diet

The low diet similarity and interspecific differences in diet diversity and B_i for co-occurring yellowfin and skipjack tunas indicate that the association between these 2 species is not because they feed on the same prey in the ETPO. Although both tuna species are considered epipelagic, and they were caught together in the same sets, their primary prey were different in all 3 of the geographic zones examined. One explanation for this was offered by Giller (1984), who mentioned that subtle differences in size or morphological structures can lead to differences in the prey consumed and reduce competition and facilitate coexistence. In the case of yellowfin and skipjack tunas, diet differences may be related to differences 1) in the anatomy of the gill raker apparatus of the species (Ankenbrandt, 1985), and 2) in body size (Graham et al., 2007). For example, Magnuson and Heitz (1971) attributed the presence of euphausids (e.g., *N. simplex*) in the stomachs of skipjack tunas in the ETPO and their absence in the stomachs of yellowfin tuna (that consumed fish) to the small size of euphausids and to the smaller gaps between gill rakers in skipjack tuna compared with those in yellowfin tuna.

Body size and morphological differences between these 2 tuna species, as described above, are possible reasons for the observed differences in the prey consumed that likely reduce competition and facilitate coexistence. Therefore, an alternative hypothesis to explain the occurrence of mixed schools is that these 2 tuna species accompany each other to protect themselves from predators, as has been suggested for dolphins and tunas (Scott and Cattanach, 1998); however, more studies on this issue should be carried out in order to clarify this unique behavior.

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